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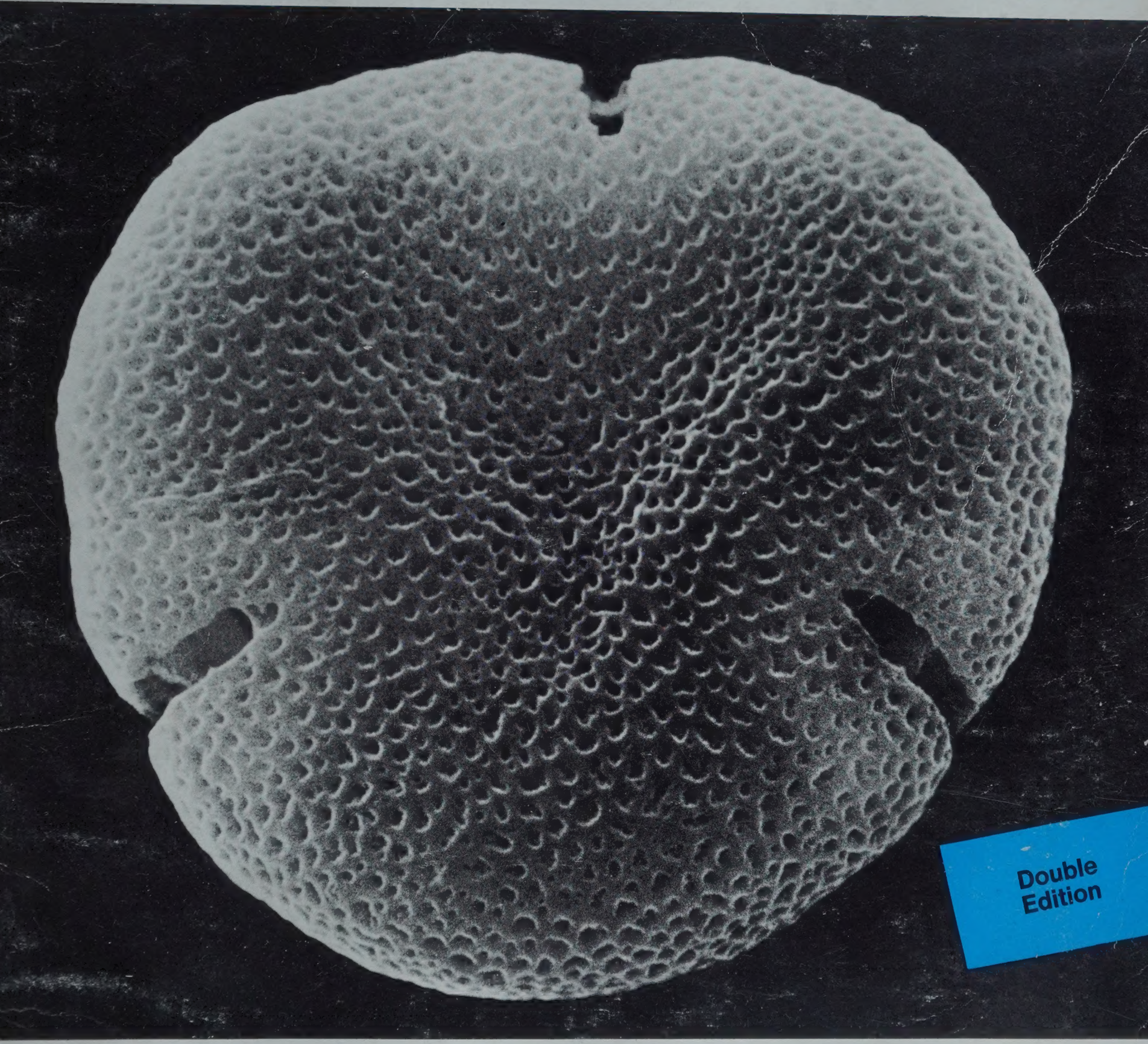

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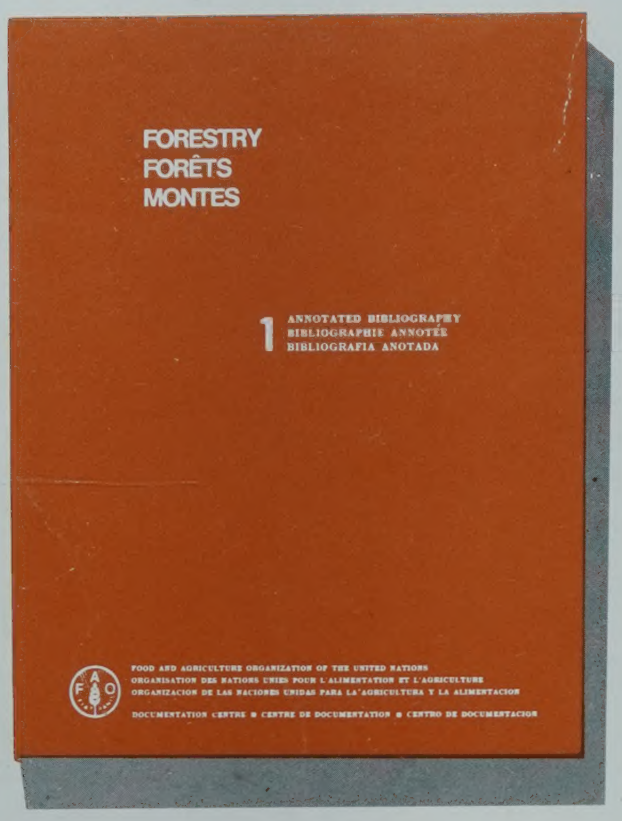
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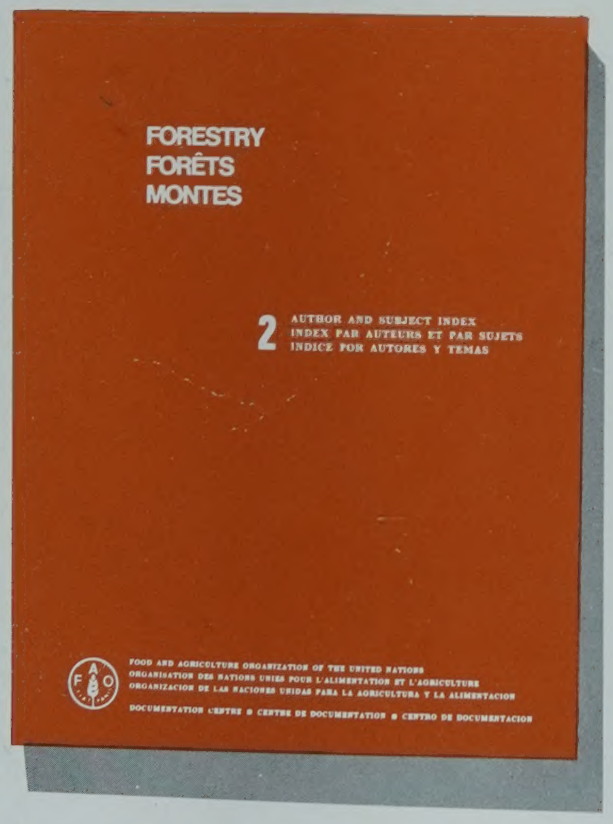
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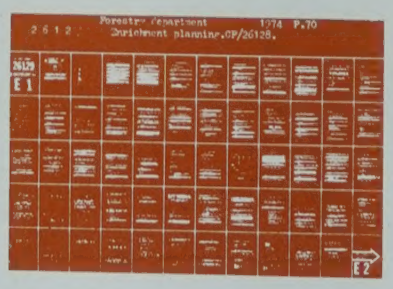

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vol. 30 no. 119-120


**Selected papers from the third World Consultation on Forest Tree Breeding**


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COVER: Pollen from a linden tree (*Tilia cordata*) seen through electron microscope

Photograph from Finnish Forest Research Institute


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the third

# World Consultation on Forest Tree Breeding

## introduction

**promises and predictions**

The third World Consultation on Forest Tree Breeding was held in Canberra, Australia, 21-26 March 1977, at the kind invitation of the Australian Government and in response to a recommendation made by the previous consultation convened in Washington, D.C., in 1969. The consultation was organized jointly by the Australian Government, the International Union of Forestry Research Organizations (IUFRO) and the Food and Agriculture Organization of the United Nations (FAO). Accommodations were generously provided by the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Canberra, with study tours arranged and hosted by the Papua New Guinea Office of Forests, the New Zealand Forest Research Institute and the forest services of the Australian states of New South Wales, Queensland, Victoria and Western Australia and the Australian Capital Territory. Much of the success of the consultation can be attributed to the efficient organization of the study tours and to the meticulous care taken by the Australian organizing committee in planning arrangements in Canberra. Grateful acknowledgement is also made to the Australian Development Assistance Agency for organizing an international training course on forest-tree breeding in conjunction with the consultation which enabled a number of participants from developing countries to attend the consultation who might not otherwise have been able to do so.

**a catalyst**

This third consultation, which brought together nearly 200 scientists and foresters from about 50 countries as well as representatives of FAO and IUFRO, was the latest in a series of international technical consultations in which FAO and IUFRO have cooperated. The first consultation in Stockholm in 1963 summarized information on the scientific principles of forest genetics and tree breeding and has been described as "hopeful". The second consultation in Washington in 1969 concentrated on the practical advantages of tree breeding and the means for large-scale production and utilization of high-yielding varieties and has been described as "full of promises and predictions". The third consultation perhaps will be viewed as catalytic as it focused on the need for more comprehensive breeding strategies and called for greater international cooperation, particularly in gene conservation and breeding of tropical species.

**insurance policy: conservation of genetic diversity**

In the last eight years notable advances have been made in the techniques of tree breeding, very much in keeping with the expectations of the Washington meeting, while there has been increased awareness of the need for gene conservation. Much of the tree breeding expertise and investment is still concentrated in the temperate zone, with the major emphasis on conifers, although in recent years evidence of the potential for rapid gains in the tropics and sub-tropics has led to a growing number of new breeding programmes in these zones. Many of these newer programmes are concentrating on broadleaved species as well as on conifers and are described in papers presented to the consultation. At the same time, the need to conserve genetic diversity for its insurance value, as an essential complement to developing superior genotypes for specific purposes, has assumed great significance. Attention has been focused on this problem by the FAO Panel on Forest Gene Resources, and by the interest in, and financial support given to, forest genetic resources by the United Nations Environment Programme (UNEP).

**superior genotypes for specific purposes**

In his keynote address to the consultation, Dr. B.J. Zobel, E.F. Conger Distinguished Professor of Forestry at North Carolina State University, presented a broad and forward-looking view of the challenges facing land managers

in general and tree breeders in particular in improving the quality of man's life. This set the stage for a technical review of recent advances in tree improvement, current problems and future prospects which was developed in technical sessions concerned with (i) exploration, utilization and conservation of gene resources, (ii) advances in species and provenance selection, (iii) population improvement, (iv) constraints on progress, and (v) analysis of the benefits and costs of tree improvement. The sixth technical session, choosing strategies for the future, drew together information from the earlier sessions and attempted to indicate the types of strategies and action programmes needed over the next decade if, in a world of shrinking forest land, tree breeding is to make its full contribution to the sustained supply of forest products and services essential for man's well-being.

**tree breeding to improve the quality of man's life**

It was fitting for a tree breeding consultation held in Australia that the technical sessions were complemented by a special invited lecture delivered by Emeritus Professor L.D. Pryor, of the Australian National University, on the reproductive habits of the eucalypts in relation to introduction and improvement throughout the world.

Each technical session was introduced by a position paper of global coverage written and presented by a senior rapporteur. The position papers, modified in the light of the discussions, form chapters of the present report. Special invited papers of more limited scope relevant to the topic of a session were presented by co-rapporteurs. These were followed by a discussion period, chaired by a technical chairman. After the discussions, the technical chairman and rapporteurs of each session drafted recommendations, which were amended and approved in the final plenary session. They are reproduced in this report along with the keynote address, the special invited lecture and the position papers. Also included is a list of the titles and authors of all papers presented, a list of officers and participants and a report on progress made on recommendations from the second consultation. The complete consultation proceedings are being printed by the CSIRO in Canberra.

**choosing strategies for the future**

During the period of the consultation, there was an interesting half-day tour to see the Australian National University's work on resistance breeding in poplars and to view examples of tree improvement of *Pinus radiata* and natural eucalypt forests in the Australian Capital Territory. Four pre- and two post-consultation tours demonstrated the considerable progress made in breeding with a variety of species in the Australian region. A pre-consultation tour to Papua New Guinea showed natural stands and plantations of araucarias and breeding and provenance work involving teak, araucarias, and tropical pines. Grafting techniques are well developed for araucarias while promising results have been obtained from controlled pollination crosses of *P. merkusii*. Teak breeding is well advanced, with a seed orchard producing improved seed.

**an impetus for tree-improvement programmes**

Participants in the New Zealand tour were greatly impressed with the scientific basis of the tree-improvement programme in that country, a programme which has provided important impetus to other work throughout the world In New Zealand a major industry based on a single-species forest crop has developed in a relatively short time. The first-rotation plantations of *P. radiata* have been screened for superior phenotypes, and a comprehensive progeny testing programme is now in progress. These tests are providing material for the advanced-generation breeding strategies now being implemented in New Zealand.

**advanced-generation research**

A pre-conference tour to northern Queensland concentrated on breeding

**clonal seed orchards**

*P. caribaea* in tropical and sub-tropical latitudes. Valuable results have been obtained from provenance and breeding studies of *P. caribaea* var. *hondurensis* in a relatively short period. Of particular interest were the clonal seed orchards of *P. caribaea* var. *hondurensis* and the potential of inter-varietal hybrids involving var. *hondurensis* and of the interspecific hybrid with *P. elliottii*. The itinerary included a visit to the CSIRO Division of Forest Research regional station at Atherton where work is in progress on taxonomy, flowering and ecology of indigenous tropical hardwoods.

In the tour of southeastern Australia, visitors were able to see native eucalypt forests which varied greatly in both morphology and productivity. Progress in pine breeding was well illustrated in programmes which are beginning to implement advanced-generation strategies. The breeding programme with *Eucalyptus regnans*, involving extensive new studies of the species throughout its natural range and a seed orchard operation, was of particular interest.

**there is ample economic evidence to justify tree breeding**

Two post-consultation tours took place: one to northern New South Wales and southern Queensland, the other to Western Australia. Near Coffs Harbour in N.S.W. the participants saw nursery and establishment techniques as well as tree improvement work which included an interesting demonstration of the possibilities of tissue culture. A high-point was the visit to the impressive natural forest at Bruxner Park. In southern Queensland the now well-known work with southern pines from the United States was inspected. The field trials of this programme provide ample economic evidence to justify the continuation of tree breeding.

The tour to Western Australia concentrated particularly on the breeding of *Pinus pinaster*. This programme is an unusual one in that it incorporates selections from a gene pool established in Western Australia many years ago as well as material carefully chosen in Portuguese forests and imported as scions and pollen. Impressive gains, particularly in stem straightness, have been obtained.

Informal evening meetings of IUFRO working parties were held during the period of the consultation on reproductive processes (S 2.01-05, 22 March), breeding Monterey pine (S 2.03-09, 22 March) and eucalypt provenances and breeding eucalypts (S 2.02-09 and S 2.03-10 jointly, 24 March).

**possibilities of tissue culture**

In addition, the Australian Forest Research Working Group on Forest Genetics met in Canberra immediately preceding the consultation (20 March), and a joint meeting of IUFRO working parties on tropical species provenances (S 2.02-08) and breeding tropical species (S 2.03-01) was held in Brisbane, 4-7 April, following the post-consultation study tour to northern New South Wales.

In conclusion, the spirit of the consultation was captured in the closing address of Prof. Max Hagman, who, on behalf of IUFRO, said:

" ... It is our obligation as thinking men to consider what in our work will be of good for society. When the first explorers went out from the old world most of what was beyond the horizon was unknown. In our days the geographic exploration of land is almost finished and only the deep sea, the blue continent, remains.

" This blue sea does not only surround the wonderful continent of Australia, it also unites all of us. This unity has been expressed since ancient times in the cooperative spirit and freedom of the men of the sea. There is, however, another ocean in which the same freedom and spirit exist: the green ocean of the forest. Trees do not recognize political borders; neither should science ...

" I think we have all noted that the ocean of knowledge is only slightly touched yet. I feel that it is the opinion of this consultation that at least some scientists should endeavour to leave the familiar green shores and go out on the deep sea of the unknown and that they should look for the *terra incognita* that may lie beyond the horizon of the things we know today.

" I cannot say what gains such an expedition may bring back since man is small and that sea is so large. I can only assure you, quoting from T.S. Eliot, that 'We shall not cease from exploration, and the end of all our exploring will be to arrive where we started and know the place for the first time.' "

**trees do not recognize political borders**

■

Keynote address

# The good life... or subsistence

## Some benefits of tree breeding

**Bruce J. Zobel**

Almost daily one is reminded of the possible crises we may face as the result of an increase in world population and the overall improvement in the standard of living. The concern is nearly always about limitations of the food supply, a recognized and very critical problem. Having enough food alone, however, does not ensure a satisfying existence — products of the forest are a key ingredient of the good life compared to mere subsistence living.

The greatest resources in the world are people and land and the destiny of the human race is determined by the way a large proportion of the world's land areas is clothed in forests of various types; thus, much of the responsibility as to whether we live fully or merely subsist is in the hands of those whose job it is to manage forest lands. We are dealing with an inexhaustible and renewable resource provided by nature. We foresters are aware of our responsibility to manage it wisely so as to obtain the maximum value to mankind while still making sure the forest resource is continuously improved and not depleted or destroyed.

One characteristic of a developing society is its increased usage of fibre products, chief among which is wood in its many forms. It is a certainty that demands on the world's forest lands will become greater while the area available for forest production will decrease. The question facing us is not whether to use the forest resource but how to use it wisely for the greatest benefit to man in the long term. If we as foresters fail, not only will our descendants be deprived of the opportunity for the "good life" and must lead a life of mere subsistence but there is doubt that they can even survive.

There are many challenges to those who manage forest lands; two of the most important are:

First, the forest land resource is finite and foresters must use what is available completely and efficiently while still maintaining it in a renewable state. The current wastage of usable timber plus locking up the renewable forest resource for essentially no use to society is inexcusable and a sin toward mankind. The utilization of forests can vary from wood products to chemical and energy production, to recreation, to watershed management; no one use is so all-important that it relegates all others to inferior positions. Because of the renewable nature of the forest resource, the same goods and services will be available after utilization as were present before, if proper management is practised.

Second, wise use of the forest resource does not imply keeping it in exactly the same state as it was prior to management. Nature's "objectives" are not always compatible with the best interests of man; a forester's mission is to make the forest land more productive of the goods or services it is most suited to supply. Sometimes this only requires retaining the forest in its original state, but usually change is required. A surprisingly high proportion of the world's forests have already been greatly (and unfortunately sometimes irreparably) changed by man's past activities in the form of fire, overgrazing, ex-

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Bruce J. Zobel is E.F. Conger Distinguished Professor of Forestry at North Carolina State University in the United States.

ploitation without regeneration — and, yes, in a few instances, even by over-protection. We, as foresters, have a primary responsibility to put unused or partially utilized lands into production. This includes managing already productive lands so that they can become even more productive. Most forest land in the world can be improved by sound management but foresters have a most difficult task to convince laymen (and unfortunately sometimes other foresters) that the best action is not "to leave the forests as nature made them" or "the best action is no action."

### Biology of forest growth

To be successful in their management efforts, foresters must learn much more about the biology of forest growth and development. They must become skilled practising ecologists. A forest is a dynamic, ever-changing complex biological system, and continuous management is necessary or it may soon no longer be ideal for the objective originally intended. It is sad, for example, to observe the consternation and disillusionment of one who has "preserved a virgin stand of timber for perpetuity" when he sees the old trees die and the idyllic, parklike vista become filled with invading briars, brush and small, unwanted, tolerant trees. Only with management could the original condition be maintained.

Although I am acutely aware of the many uses and services from forest lands other than timber production, including recreation, aesthetics, water quality and others, I must concentrate on one major forest product to meet space requirements for this paper. Since my main expertise is in growing trees to produce timber and cellulose, the following discussion will concentrate on this area, although many of the principles will apply to all aspects of forest land management.

There is a tendency for foresters concerned with timber production to specialize either in utilization and harvesting or in the general area of forest management. This is the wrong approach and we never will obtain the full timber production from forest lands until there is a "marriage" of all expertise, a happy marriage where all contributions are together for the common goal. If, for example, logging is separated from silviculture, great inefficiencies will develop; what the silviculturist can or cannot do is strongly influenced by the logging system applied prior to regeneration. Careless logging can so drastically change the site potential and reduce site index that the strain or species initially growing in the area is no longer suitable. It is inexcusable for the silviculturist to be faced with major problems limiting regeneration and future growth just because a logging method harmful to the site was used through ignorance, lack of concern, or economic pressures.

### Another tool

In the same way, methods of forest management must be used to supplement each other. Thus, genetics without good site preparation or competition control will be ineffective while fertilization without use of the best genetic stock or site preparation can only be partially successful.

In its broadest sense, genetics is only another tool of silviculture used to obtain greater production from forest lands. Considered alone, genetics verges on the academic; used along with proper site preparation, competition control and fertilization, it is the key to maximum production of timber from forest lands. Even though it must be viewed as a silvicultural tool, genetic manipulation of forest trees has certain unique characteristics:

- A genetic change is "permanent" in that it need not be repeated once or several times during each rotation, such as does fertilization, competition control, or site preparation.
- As the most productive forest lands are converted to agricultural or other uses, new strains of forest trees can be developed which are adapted to currently marginal or sub-marginal sites; this will enable maintenance or even expansion of the productive forest land area. Similarly, strains for special products can be developed.
- Most insect or disease pests can be efficiently controlled only through developing tolerant strains of trees. Even when controls are known they often are too expensive or difficult to apply or are considered to be too ecologically dangerous to use over extensive forest plantations.
- Through the eons, nature has developed numerous types of trees with greatly differing genetic potentials. It is the responsibility of the tree breeder to recognize, refine and use these for the benefit of man. With forethought and planning the bulk of the gene base can be preserved for new needs that might develop in the future.
- Through selective mating and hybridization it is possible to create "something new," trees with characteristics not available from nature. This ability to tailor-make trees is gaining increased consideration as the variability present in natural forests becomes more widely exploited and ultimately eroded in selective breeding programmes.

Development of desired characteristics through genetic manipulation has given the forest manager a most useful, powerful, and efficient tool to add to other silvicultural methods at his disposal. In certain problem areas the tree breeding approach has revolutionized the thinking and methodology of the forest manager.

The current trend to establish fast-growing conifers and hardwoods in plantations in the tropics will increase.

### Unique opportunity

Because of ease of establishment, emphasis has been on planting on grassland or scrub hardwood sites; however, replacement of tropical hardwood forests by plantations on the most suitable sites is rapidly gaining momentum. In either case, exotic species are generally used, presenting a unique opportunity for the use of genetic manipulation; in fact, success or failure of tropical plantations is more dependent on proper application of genetic knowledge than on any other factor.

The forester contemplating establishing fast-growing plantations in the tropics is, of course, faced with a decision as to which species to use; of

MATURE HARDWOOD STAND GROWING IN A SWAMP

*there is much to be learned*

equal importance is the decision as to which geographic source is most suitable within the desired species. Seed source is more critical to success in the tropical areas than in the more temperate forest regions. Once species and source have been determined, then improvement by conventional selection and breeding is necessary if maximum timber production is to be obtained.

A problem often requiring major genetic manipulation relates to pests that will attack exotics. Plantations in the tropics may be pest-free for a few or even for many years, but a certainty is that either a native pest will adapt to the exotic or a pest of the exotic in its natural range will somehow follow the species into the new environment. Usually the only effective way of combating such pests is to develop trees that are genetically tolerant.

A most pleasing recent trend has been the change of attitude by key foresters and administrators regard-

ing the place of tree breeding in forest operations. Initially many considered it to be research, something with little potential for practical usage. During the past 10 years this attitude has dramatically changed, and many industrial, as well as governmental, programmes now include tree improvement as an integral part of their forest management operations.

One major reason for acceptance of tree breeding in forestry is that it has proved to be a good economic investment. Every economic study of the value of tree improvement with which I am familiar (and that has been many) has shown that genetic manipulation of forest trees yields excellent returns on the investment. Several analyses have concluded that tree improvement is the best possible investment in the whole forestry enterprise.

Tree breeding programmes are well developed in several parts of the world, with advanced-generation breeding already under way. The most urgent need for expansion of effort is in the tropical areas where so much forestry activity is now taking place. For example, seed of species such as *Pinus caribaea* is in short supply and genetically improved seed is unavailable. Despite its importance it is often not possible to obtain seed from the correct geographic source and much planting is being done using ill-adapted stock. This poses grave danger when large planting programmes are developed and then abandoned, because of failure caused by use of the incorrect seed source. Such a catastrophe can reduce interest and faith in forestry as a sound investment, and several examples of an adverse reaction which set forestry back many years could be cited. The seed problem for tropical areas is especially difficult because it is necessary to cross boundaries of one to several countries if success is to be achieved. With fast-growing species the payoff from the use of genetics will be especially large and rapid if the considerable difficulties can be overcome by means of a cooperative effort.

There is no question that the future of the application of genetics to forest trees is very great. There will be expanded and better supported efforts throughout the world as the need to increase yields from forest land becomes more widely recognized. In some areas the applied programmes are beginning to outstrip the needed base of fundamental information, with the result that certain inefficiencies are developing. Thus, one of the major needs in the future is a greater emphasis on supportive, basic studies necessary to undergird the application phases of tree breeding. The days of straightforward selection and seed orchard establishment are drawing to a close in a number of areas and more sophisticated developmental techniques will be required if tree breeding is to continue making gains without interference from the adverse effects of related matings.

There is no question about the need for increasing emphasis on fast-growing plantations, especially as exotic plantation forestry intensifies. Another urgent need is to work with indigenous tropical species, some of which appear to have outstanding potential although little is known about their silvicultural or genetic characteristics. The huge area of the tropics with plentiful rainfall and soils generally suited for forest production must contribute its share to the welfare of man. In general the hardwoods as a group have been neglected, although progress in breeding the eucalypts has been outstanding.

New methods and new techniques of tree breeding must be developed; for too long we have followed the methodology used with agricultural crops. Trees present unique opportunities and advantages if we learn to develop them correctly. As an example, much of the quantitative theory on which forest tree breeders rely is based upon control of important characteristics by single or few genes. Yet many of the most important tree characteristics are determined by complex genic and allelic interactions and the developed theory can only be partially effective. Great emphasis is already being placed on ways to speed up generation turnover and to develop good methods of obtaining juvenile-to-mature correlations. Once accomplished, breeding results and gains per unit time can be greatly improved.

A most important trend is the increase in efforts to develop trees that will produce a useful crop on marginal or submarginal forest land. Land-use pressures and environmental controls require change in the land area that will be used to produce forest products. If forestry is to supply its share of the world's fibre needs, new genetic strains must be tailor-made for currently marginal areas; with the uncertainty about the future cost and availability of fertilizers, strains of trees need to be developed that will grow satisfactorily on soils of low fertility. The success in developing special strains of trees suited to difficult conditions has been outstanding. Directly related to this, an increased tempo toward breeding for resistance to pests is sure to develop.

There will be greater efforts and demands to develop trees better suited for urban usage or for amenity forests. Methods and objectives will vary considerably from breeding for forest production but, because of the high value of the individual tree, techniques can be used that are now viewed as unsuitable.

During the past several years much interest has developed toward using wood in nontraditional ways. Methods are now known to efficiently produce petroleum derivatives, plastics, and sugars from wood. No one yet knows whether manufacture of such products from wood will become generally operational, since it is dependent on the many vagaries of economic conditions, petroleum prices or other factors. If these uses of fibre develop, a new emphasis on cellulose production *per se* will become evident. We have already been contacted several times by organizations interested in the most efficient way to supply cellulose, regardless of the form of the plant which produces it.

A major effort of tree breeders in the immediate future will be to conserve the genetic base necessary for long-term and continued progress. Forest trees have a very rich store of varied gene complexes that must be preserved for future generations. Erosion of the genetic base will not result so much from breeding programmes *per se* but from indiscriminate exploitation of the forest resource. Conservation of the gene complexes within

GRASSLAND BEING PLANTED TO *Pinus caribaea*
*changing horizons*

a species can be done by several methods but all are expensive. Care must be taken to avoid the panic measures promoted by preservationists in which nonsense laws, rules or regulations are enacted in the guise of gene conservation. This has resulted, for example, in removal of huge areas of tropical hardwoods for use as timber products. Rather than locking up such forests, we need to learn how to use their products for society while at the same time preserving the best of the tremendous store of available genetic variability. It is the duty of everyone involved in tree breeding to do his share to assure the conservation of desired gene complexes.

As the world population and standard of living increase, greater demands will be made on all benefits from land. Demand for wood per se will greatly increase if society is to satisfy its needs for a better standard of living, of which fibre is an integral part. As forest land becomes diverted to other uses, a major need will be to increase production on the land available and to develop strains of trees for currently marginal and submarginal sites. This can be done by better utilization combined with better forest management and silviculture. One of the most effective tools of the silviculturist is to use the variation found in forest trees through tree breeding programmes; however, maximum gains can only be achieved if all the tools of silviculture are used to supplement each other. Operations in tree breeding are being greatly accelerated as the gains achieved and good economic returns are recognized.

There is a special need to develop genetically improved material for fast-growing plantations of exotics in the tropics. Seed of the proper geographic source is difficult to obtain and very little genetically improved seed is available. A cooperative approach which crosses national boundaries is essential if this most important endeavour is to be successful.

The future development of tree breeding needs emphasis as follows:

- More supportive basic research is essential if the applied programmes are to proceed with the desired speed and efficiency.

- There needs to be much more effort on improvement of geographic source and individual tree characteristics for fast growth plantations in the tropical areas.

- New techniques need to be developed so that tree breeders are not so dependent on methods developed for agricultural crops, many of which are not suitable for the gene complexes which control important characteristics in forest trees.

- There needs to be a greatly expanded effort to develop trees for sites now considered marginal or submarginal; a companion effort is to develop strains tolerant to pests.

- If nontraditional uses of cellulose such as for plastics, sugars or energy become generally operational, a great emphasis will deal with the production of maximum amounts of cellulose, regardless of the form of the plants which produce it.

- Major efforts will be needed to conserve important gene complexes which are necessary for continued and expanded progress in tree breeding.

Forest tree breeding has developed rapidly but the horizons for the future appear to be almost limitless. It is a most important tool to help members of society enjoy the good life rather than exist on a subsistence level. ■

# Exploration, utilization and conservation of genetic resources

**R.H. Kemp**

The period since the last World Consultation has seen much activity, from the work of individuals and research institutes to the national and particularly the international scale. The developed countries, mainly in temperate regions, have been largely responsible for the elaboration of the philosophy and strategy of genetic conservation, and they have to a large degree the means to explore and conserve their plant genetic resources in their own interests, both severally and in collaboration. It is in the tropics and sub-tropics that the greatest potential exists for development of forest genetic resources, and it is also there that action on conservation is most urgently needed.

The FAO Panel of Experts on Forest Gene Resources initiated in 1968 an action programme of exploration and seed collection, which has been implemented through the work of research institutes and organizations, with a large financial contribution from bilateral aid funds, as well as some from the FAO regular programme (FAO 1969, 1972, 1974a, 1975a, 1976). In addition the Panel has helped to achieve the still growing acceptance that the conservation of forest genetic re-

NICARAGUAN FORESTER SEARCHING FOR *Pinus pseudostrobus* SEEDS

*special skills*

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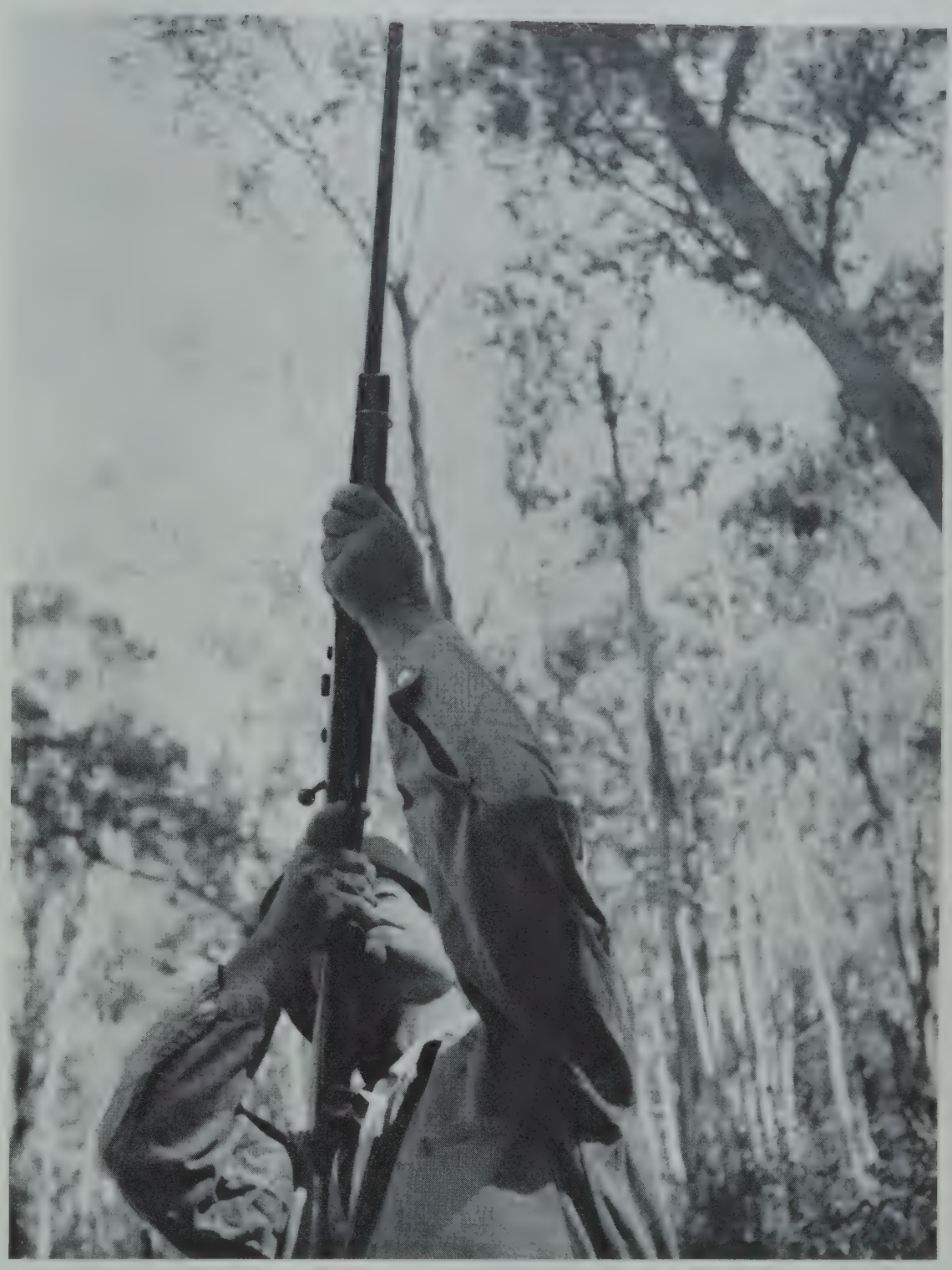
sources is a matter for global concern and action. This concern received expression at the United Nations Environment Conference at Stockholm, in 1972, and in the Global Programme for Improved Use of Forest Genetic Resources (FAO, 1974b), but action to conserve genetic resources on the scale required and recommended by the Panel has scarcely begun.

The problems of both exploration and conservation are different for a species whose natural range is restricted to a single country from those of a species which extends through many different countries, perhaps on different continents (Koster, 1977). The earliest schemes of international cooperation were between countries equipped and interested to exchange seed from their own sectors of a species' range. Cooperative action through the International Union of Forest Research Organizations (IUFRO) has been very successful and has embraced a further development, whereby one institute may undertake seed collections on behalf of several countries, including its own, which are interested in the species. Such expeditions (e.g., Barner, 1971) have been influential in the development of procedures, in revealing problems and in setting standards.

Some countries, with well-developed forestry services, already concerned with exploration and seed collection, provide material for international distribution, as seen in the work of the Poplar Council and the U.S. Forest Service Tree Seed Service Centre, or the Seed Centre of the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Australia. The programme on eucalypts started by the Forestry and Timber Bureau, and continued by CSIRO (Turnbull, 1977), has been of the greatest importance for many developing countries which otherwise would not have had access to this valuable material. The modest financial contribution from FAO is an example of the most effective use of the limited international funds so far available.

Even for Australia the extent of the exploration required is an immense task, in its demands on the time of skilled staff, as well as the financial cost. An example of cooperation is seen in the seed collection mission of the French Centre technique forestier tropical (CTFT) to Australia, Timor and Indonesia in 1973 (Cossalter, 1974). Although this mission was undertaken primarily for the benefit of the countries where CTFT is involved in research programmes, many other countries may also benefit. As a result of trial plots, and some larger stands, hitherto unavailable provenances of tropical eucalypts have now been established in Africa for the first time, and these few exotic populations will become local sources for wider distribution of reproductive material to other African countries in the future.



AUSTRALIAN FORESTER SHOOTS DOWN BRANCHES FOR SEEDS
*aiming for high quality*

Very few developing countries have the resources to undertake exploration and seed collection outside their own borders, and even within their own countries they have other prior demands on limited staff and funds. In these circumstances the programme recommended by the FAO Panel, and mainly financed and executed by bilateral aid organizations, notably in Denmark and the United Kingdom, has had the greatest success in recent years (Keiding and Kemp, 1977; Wood and Greaves, 1977). As a result of this work nearly 50 countries in the tropics and sub-tropics have been able to establish provenance

trials of promising fast-growing species, including many provenances never previously collected. The trials show that some of these are distinctly different from and markedly superior to earlier introductions of the species (Keiding and Kemp, 1977). In order to complete range-wide provenance sampling, and to meet demands for trials and the further needs for gene conservation, several years of seed collection are normally needed. In some cases local seed centres have been established in association with the overseas institutes conducting exploration and seed collections, with bilateral aid funds, and this development offers the best prospects for future supplies of seed.

New thought has been given to the study of genetic variability and its implications for exploration. The theoretical basis of sampling strategies for crop plants has been examined in recent papers (see Hawkes *et al.*, 1976), many of which are relevant to exploration of tree species (see also Stern and Roche, 1974). However, basic information on patterns of variation, flowering and fruiting behaviour and breeding systems is lacking, especially for tropical tree species. For this reason most exploration has been guided by general principles, modified by the practical necessities imposed by local conditions (Kemp, 1976). The explorations made have added greatly to previous knowledge, through collection of ecological and distribution data, herbarium samples and biochemical samples (*e.g.* pine resin) for taxonomic studies.

The international programmes in which the distribution of seed and coordination of trials are centralized, have opened new possibilities for genecological studies, as well as for the evaluation of provenance and environmental interaction (Burley and Kemp, 1973). They have made necessary the development of computerized systems for data storage and retrieval (*e.g.* Burley *et al.*, 1973). Advances have also been made in methods for rapid evaluation of large numbers of wood samples from trees under the influence of the environment at the site of introduction (Hughes and Andrew, 1974). Through the collaboration between the institutes conducting and coordinating the research, and the nearly 50 tropical countries carrying out the field trials (see Wood and Greaves, 1977), new possibilities exist for the early recognition of populations deserving priority for further collection and gene conservation.

Recognition of the need to conserve forest genetic resources has widened and much thought has recently been given to the methodology of conservation, both *in situ* and *ex situ* (e.g., Fowler and Yeatman, 1971; Roche *et al.*, 1975). Individual countries with adequate means to explore and protect their genetic resources are already taking such action in their own interests, and thereby helping to demonstrate and test the methods used (*e.g.* Hagman, 1971). In some cases neighbouring countries are co-operating in the compilation of lists of threatened species, and in the conservation of their genetic diversity, for example, Canada, Mexico and the U.S.A. (Barber and Krugman, 1974). Species known to be in serious danger are recorded in the International Union for the Conservation of Nature and Natural Resources (IUCN) Red Data Books, while others not severely endangered as species, but undergoing serious genetic impoverishment in some part of their range, are included in a series of data sheets produced under the auspices of the International Union of Forest Research Organizations (IUFRO) Working Party on Gene Resource Conservation (FAO, 1974c).

**Basic information on patterns of variation, flowering and fruiting behaviour and breeding systems is lacking, especially for tropical tree species.**

In many tropical and sub-tropical countries the means are very limited, and international assistance, both financial and operational, has been proposed (Kemp *et al.*, 1972; FAO, 1974b). Effective financial support from international organizations has yet to be secured. However the Governing Council of the United Nations Environment Programme (UNEP) decided to allocate funds to support conservation of genetic resources, during its first biennium, and subsequently UNEP agreed to finance a short term pilot study on "The Methodology of Conservation of Forest Genetic Resources" (Roche *et al.*, 1975). Following the recommendations of this study, which supported recommendations made earlier by the FAO Panel (FAO, 1974b), a new project for the "Conservation of Forest Genetic Resources", submitted by FAO in June 1975, became operational in the second half of 1976.

As noted by Frankel (1977) secondary gene pools of a number of tree species already exist in many countries through the widespread use of exotics in plantations. These are normally managed, and their genetic resources are therefore influenced by production criteria, and the idea of plantations specifically to conserve forest genetic resources is comparatively recent (e.g. Bouvarel, 1970). The FAO Panel (FAO, 1974b) recognized the international responsibilities involved and the principles and methods were fully discussed by Guldager (1975).

The project, as accepted by UNEP, constitutes the pilot stage of what is hoped to be an expanding, long term programme, and at present has a duration of only two years. The main emphasis is on action *ex situ*, through support for seed collection and the establishment of conservation stands in 10 tropical countries. The species proposed by the FAO Panel were chosen partly because of their proven importance and partly because seed of some of the most valuable and endangered provenances was already available from collections made by the Commonwealth Forestry Institute, Oxford (C.F.I.) and the CSIRO. During 1977 the distribution of seed, the selection and preparation of sites, and the raising of nursery stock for the conservation stands will be well advanced in several countries. Limited provision was also made to assist with conservation *in situ* of forest eco-

systems in India and West and East Africa, but in this field dramatic achievements cannot be expected in such a short period.

Another field in which achievements have been made is seed research and seed storage. The seed of many fast growing plantation species can be readily stored for long periods, often for decades, without serious loss of viability or other apparent deleterious effects. However there are other species, particularly in the tropical rain forests, whose seed loses all viability within a few weeks, or even days, after seed fall, under normal conditions. This has been a major constraint on the use of such species in plantations, especially as exotics. Much information has recently become available, particularly in agricultural practice, but often of relevance to forestry (*e.g.* Harrington, 1970, 1972; Roberts, 1972, 1975; Wang, 1974, 1975; Barner, 1975, Turnbull, 1975).

Frankel (1977) has drawn attention to the new techniques in prospect for the storage of "recalcitrant" seeds (*e.g.* Villiers, 1975; Sakai and Noshiro, 1975). Although such fundamental studies will no doubt concentrate on agricultural seeds, the results are likely to improve the prospect for long-term storage of forest tree seeds, and may be particularly important for many tropical rain forest species. Little or nothing is known at present about the behaviour of the seed of many such species, and the way it may be affected by the treatment given during collection, handling and storage. The need for more studies of tropical tree seeds was stressed at the IUFRO International Seed Symposium, in 1973 (Simak and Kamra, 1973; Kamra, 1974) and at the International Seed Testing Association (ISTA) Workshop on Forest Tree Seed Testing, 1975.

Important advances have been made in the successful storage of seed which, while they are essentially "orthodox", require special care and treatment during the critical period immediately after seed fall to bring them safely to a suitable condition for low-temperature storage. Once through-this critical period they may be successfully stored for decades, thereby opening new possibilities for conservation and utilization. An example is the work on the seed of *Agathis* spp. As a result new possibilities exist for plantation trials and genetic conservation of selected populations of this valuable genus (Whitmore, 1977).

Despite some positive achievements in exploration and conservation, the loss of forest genetic resources has increased during the past decade, and is still accelerating. This loss cannot be exactly quantified; indeed lack of precise information on the nature, location and conservation status of valuable genetic resources is itself a major problem. Nevertheless the destruction of natural forest, particularly in the tropics, is so rapid and widespread that there can be no doubt that valuable populations have already been lost in recent years and others

**The danger of destruction is most severe in the tropical rain forests, even in protected areas, as the natural forest is increasingly converted to high-yielding plantations. It is happening in Africa, in the Amazonian rain forest, in southeast Asia.**

are severely threatened. The danger is probably most severe in the tropical rain forests, since these are not well represented in the U.N. List of National Parks and Equivalent Reserves, 1975. Some areas which have hitherto received selective protection within forest reserves are now threatened, as the natural forest is increasingly converted to high-yielding plantations, often using exotic species (Kemp *et al.*, 1975). This process is evident and rapidly increasing in many African countries, while elsewhere areas such as the Amazonian rain forest, which had previously been protected by their inaccessibility, have recently been exposed to exploitation and massive clearance of forest. In South-East Asia it has been estimated that the entire timber resources of the tropical rain forests are unlikely to last beyond the end of the century (Whitmore, 1975). Owing to the great diversity of species in the rain forests, and the almost complete lack of knowledge of their ecology and genetics, their conservation is at present inseparable from the conservation of the ecosystems in which they occur (Roche, 1975b).

Even species and populations already proved to be among the most valuable for-high-yielding plantations are in danger (Turnbull, 1977; Keiding and Kemp, 1977). Frequently the populations most endangered are those at the fringe of the geographical or ecological range (*e.g.* Kemp, 1975) and these may be among the most valuable for use elsewhere under extreme site conditions (Koster, 1977; Holzer, 1977). There is evidence that such marginal populations are genetically different from those in the centre of the range, due to the different selective pressures for survival (Sziklai and De Vescovi, 1977). For species already being used in plantations there is a danger of loss of genetic integrity within local populations, through contamination from other populations introduced from elsewhere (*e.g.* Frankel, 1977; Holzer, 1977; Keiding and Kemp, 1977; Turnbull, 1977).

There are at present only twelve tropical species in major international provenance trials, and for some of these the sampling of the natural range is far from complete. With the resources so far devoted to this work there seems little prospect of adding to this number at an average rate of more than perhaps two species a year. At this rate it would take more than a century to explore and collect representative material of those species already recommended by the FAO Panel as in need of such action.

The determination of priorities in the list awaiting action is most important but in this, as in many other aspects of exploration, the lack of information is a major problem (Keiding and Kemp, 1977). Later, at the start of exploration, lack of data on the natural distribution of a species, its variability, flowering and fruiting times throughout the range, and the possibilities for access, travel and

SORTING A PROVENANCE COLLECTION OF *Pinus oocarpa* *conserving gene pools*

transport of material further compounds the practical problems involved (Kemp *et al.*, 1975). Really efficient sampling schemes can only be designed after a comprehensive study of the variation within the species but in many cases seed collection is an essential prerequisite to exploration of the genetic variation (Turnbull, 1977).

For many developing countries the need to select and multiply the most suitable high-yielding varieties, and to initiate further improvement based on these populations is immediate. However, seed of the provenances which have been proved superior in trials may be unobtainable. Even if the original population has not been entirely destroyed it may have been reduced by exploitation or forest clearance to areas of young regeneration, with perhaps a few overmature and unsound trees, or to remnant stands in remote and inaccessible situations. It has been noted that even for species of widespread importance the reprocurement of seed of provenances which have proved superior in trials in quantities sufficient to supply the needs of many developing countries is a major difficulty (Turnbull, 1977). The international programme of exploration and research, with the cooperation of many developing countries, can open the way to the creation of highly productive plantations on a large scale, but only if action is taken to ensure that sufficient quantities of reproductive material of the most appropriate provenances are available when and where they are needed (Keiding and Kemp, 1977).

Despite the immediate danger, the longer-term prospects for conservation have improved since the last World Consultation, due partly to the awakening of interest in nature conservation, and partly to the development of cooperative action within the proposed Global Programme (FAO, 1974b). The cooperative organization is still fragmentary and weak, with inadequate funds and staff, but stronger international support is in prospect.

Frankel (1977) has drawn attention to the special affinity between forest tree conservation and nature conservation, and to the possibilities for the establishment of gene pool reserves of threatened species in association with nature reserves (see also Roche *et al.*, 1975). Turnbull (1977) indicates how this approach is developing in Australia, and similar examples could be drawn from other countries. The essential need for *in situ* conservation of the genetic resources of many tropical rain forest species has been noted earlier and, when 100 to 200 tree species occur in a single hectare, while the number of breeding individuals of a species may be only one or two per hectare, this may demand the setting aside of large areas of forest. However, it should be remembered that the genes, and gene complexes, which control most important characteristics may be safely preserved in relatively few individuals, and it is generally wrong to suggest that vast areas of forest must be set aside to meet the needs of gene conservation.

The integration of nature conservation and genetic resource conservation on the global scale was taken a stage further by the formation of the Expert Panel on MAB Project 8, in 1973, and the resulting final report on this project (Unesco, 1973). A later report on the choice and establishment of biosphere reserves (Unesco, 1974) recommended the provision of international funds to assist countries in the development of reserves, specifically suggesting recourse to the advice, cooperation and assistance of UNEP. Altogether over 200 sites for biosphere reserves have been proposed by forty countries. Most of the proposed biosphere reserves are to be found within existing national parks or other protected areas and their designation may

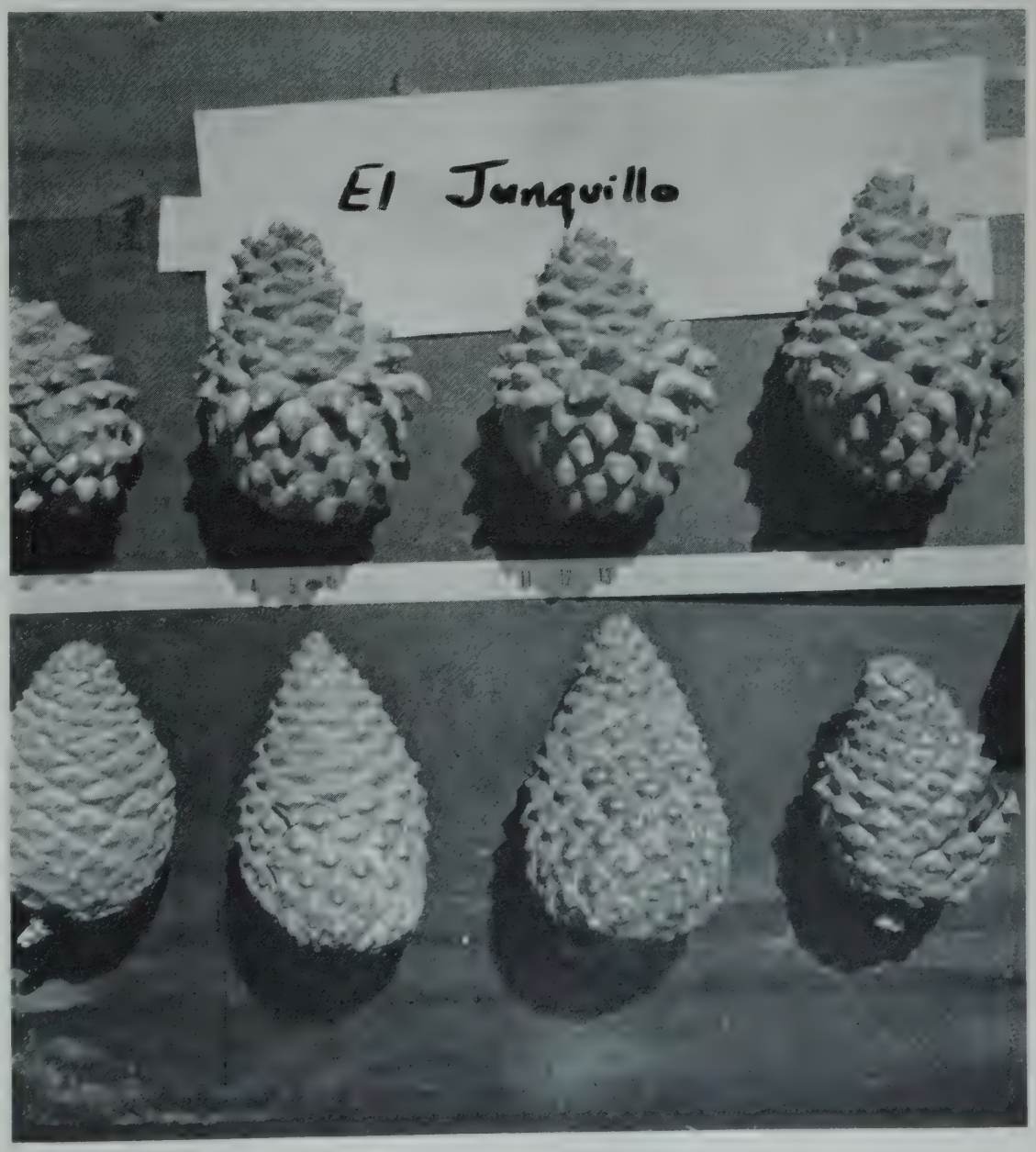
not in itself alter their previous protective status, or reduce the threat of damage or encroachment.

The International Union for the Conservation of Nature and Natural Resources (IUCN) is carrying out surveys to assess the extent to which representative samples of natural ecosystems are effectively protected in national parks, nature reserves and other protected areas (e.g., Lamprety, 1975; Whitmore, 1976). The conservation review of tropical rain forests, already completed for Asia, is being extended to Africa and America. Through the IUCN association with the World Wildlife Fund (WWF) substantial financial assistance may be secured for conservation in Indonesia and Suriname. A previous example is the creation of the Tiger Reserves in India. These are situated within existing forest reserves and include a " buffer zone ", the recommended pattern for *in situ* conservation (Roche, 1975a). Such action, in view of its very strong financial and political support, offers good prospects for effective long-term conservation of forest genetic resources of tropical forests.

However, this example also illustrates the limitations of nature reserves for this purpose, since both selection and management of the Tiger Reserves are biased toward their primary purpose. Although a well-chosen pattern of strict natural reserves may conserve the genetic resources of the important tree species in some part of their range it may fail to protect particular valuable populations of a species, for example in marginal areas. Moreover many fast-growing plantation trees are pioneers, not members of the climax communities but of seral stages, and to conserve such populations *in situ* may require precise management of the reserve, or of a sufficient part of it, to that end, for example by a regime of controlled burning. This means that informed forestry opinion must play its part in both the selection and management of the nature reserves.

The establishment of plantations for the conservation of the genetic resources of selected species and provenances *ex situ*, in a variety of environments, offers new opportunities for the expression of existing genetic diversity, and for the development of new gene combinations, in harmony with the new environments.

In the wider context of the conservation of plant genetic resources generally, a ' global network ' of genetic resources centres is beginning to emerge (Frankel, 1975) and regional centres are being developed in key areas (e.g., Kjellquist, 1975). Regional centres for collection, distribution and conservation of forest tree seed, and for associated research, have long been advocated (e.g., Hagman, 1969) and prototypes exist in several tropical as well as temperate countries, although at present these may function mainly as national rather than regional centres. The evolution of a national centre into a regional one, wherever appropriate, is probably the best method of establishment. A national centre concerned with forest genetic resources is needed in every country, although in its first and simplest form it may be only an information centre, perhaps one man, located within an existing organization, to provide and receive information as part of the international network (Kemp, 1974). In response to a circular letter distributed by FAO in 1975, over 70 countries have so far each nominated a National Coordinator of Forest Genetic Resources Information and these will in future help to identify the danger spots where urgent action is needed, as well as to assist with information needed for exploration and collection. Much information could be gathered during the course of other routine operations, and without the use of extra staff, if simple procedures were instituted. Opportunities exist in the course of forest inventories and surveys, which may have other specific




CONES FROM A SINGLE PROVENANCE COLLECTION OF *Pinus oocarpa*
*nature works through variation*

aims, but which have ready access to information and material of great value for genetic resource exploration and conservation. All that may be required is some thought in advance, for example by the National Coordinator, and the provision of briefing material, questionnaires, recording forms and collecting apparatus, as appropriate. In some circumstances extra staff, perhaps with special skills, may need to accompany the party, but there would still be a saving in cost and time compared with a separate expedition.

The Consultative Group on International Agricultural Research (CGIAR), after prolonged study, has made available funds for exploration and conservation of plant genetic resources, and is supporting the development of the global network of genetic resources centres. The funds are administered by the International Board for Plant Genetic Resources (IBPGR). Priority has, of course, been given to food crops but in February 1976 the IBPGR agreed unanimously that it should give limited support to exploration and conservation of the genetic resources of a few tree species important in agricultural connections, in addition to actual food trees. (Subject to approval in principle by the CGIAR and based on its recommendations on species made by the FAO Panel at its March 1977 meeting, it is possible that international funds might be secured from the IBPGR.) The CGIAR is also a source of funds for training and documentation in genetic resource work. These activities are urgently required in the forestry sector.

Detailed proposals for action have already been made in the Global Programme (FAO, 1974b) and, given the necessary funds, could be implemented quickly. There are several other main constraints in addition to the financial ones, particularly the lack of information, lack of skilled and experienced staff, and lack of facilities for research. The strength of the Global Programme is that it is an integrated attempt to solve these various problems in parallel, by increased provision for training, information services, research, data storage and retrieval and other related activities, in addition to the field operations of exploration and conservation. Because it is designed to draw its funds from several sources, including both international and bilateral aid, implementation has been partial and uneven, since some major potential donors, such as UNDP and the CGIAR, have yet to provide the support requested.

While every effort must be made to achieve full implementation of the Global Programme, the current economic difficulties faced by many countries and international organizations, and the prior demands for food production, will restrict the possibilities for additional funding of forest genetic resources work. It is significant that the achievements so far made are very largely the result of individual effort and enthusiasm, and the more effective use of existing staff, facilities and funds, rather than any major increase in funds available, particularly at the international level. This is above all due to the coordination achieved through the FAO Panel of Experts on Forest Gene Resources, and the work of the FAO staff who act as the secretariat, in Rome. The appointment of the National Coordinators of information in the member countries could lead to the most efficient use of already existing staff, facilities and opportunities for action in exploration, collection and research. However, most of the individuals involved in this international network have other responsibilities, often in other sectors of work, that make more immediate demands on their time. The effectiveness of the network will depend entirely on the effectiveness of the coordination, and the enthusiasm of the individuals, and these can only be maintained through very frequent and close contacts, by visits as well as by correspondence. The coordination should be provided by the FAO secretariat in Rome, but the present staff resources there are totally inadequate to undertake it effectively.

**A national centre concerned with forest genetic resources is needed in every country. In its simplest form it can only be one man, located in an existing organization, to provide and receive information as part of the international network.**

A strengthening of the FAO staff and activities in genetic resource work had been proposed and approved, but implementation of the proposed increase has been restricted in the current economic crisis.

Regional meetings and workshops can contribute greatly to the exchange of information, the maintenance of interest and enthusiasm, and the provision of necessary training. Excellent examples are the FAO/DANIDA (Danish International Development Agency) courses (*e.g.* FAO, 1974d; FAO, 1975b). To be most effective these must be held in the regions concerned, and should bring together the individuals most closely concerned with the work in their own countries. When well-staffed regional seed centres exist these can undertake such responsibilities but in the meantime the necessary expertise may be found in the institutes undertaking exploration and seed collection under bilateral aid programmes, for example in Australia, Denmark, France and the U.K. In either case provision of international funds for travel and subsistence of the participants may be needed, and the assistance of staff of the FAO secretariat in the organization of the courses is equally necessary.

Action taken during the next decade in exploration and conservation of forest genetic resources, particularly in tropical regions, will decide the continued existence, or disappearance, of many wild populations. The effectiveness of the coordination, and of the links for information and action between the areas in need and the organizations and institutes with the capability to act, will be decisive. ■

Note: References are at the back of the magazine, following the last article.

# Advances in species and provenance selection

**J.F. Lacaze**

During the past ten years numerous projects have been put into operation, very often on the basis of international collaboration. In this connection special mention should be made of the excellent work done by various bodies such as the IUFRO working groups on provenance seed collection of North American species, FAO (Committee on the Coordination of Mediterranean Forestry Research), the Commonwealth Forestry Institute, the Danish/FAO Forest Tree Seed Centre and the Centre technique forestier tropical (France).

The number of species on which provenance trials are conducted is very high; just as examples, we can list:

- For species concerning temperate zones: *Abies grandis*, *Picea abies*, *Picea sitchensis*, *Pinus contorta*, *Pseudotsuga menziesii*, *Larix europaea* and *Populus trichocarpa*.
- For species concerning Mediterranean zones: *Pinus halepensis*, *Pinus brutia*, *Eucalyptus camaldulensis* and *Eucalyptus dalrympleana*.
- For species concerning subtropical and tropical zones: *Cedrela odorata*, *Eucalyptus alba*, *E. camaldulensis*, *E. deglupta*, *E. microtheca*, *E. tereticornis*, *E. urophylla*, *Pinus caribaea*, *P. kesiya*, *P. oocarpa*, *P. pseudostrobus*, *Tectona grandis*, *Terminalia ivorensis* and *T. superba*.

In most cases the species studied are exotic to the country in which the experiments are being conducted.

The transfer of forest reproductive material, throughout the world, has reached unprecedented heights during the past few decades; many countries have been trying to intensify their forest production by introducing new species or provenances.

At the same time, there has been an increase in organized research aimed at supplying silviculturists with objective information on the vegetative material to be selected.

An effort on this scale is inconceivable without active international cooperation. Some progress has been achieved, but much remains to be done in this field.

We shall not refer to the definitions of standard terms such as "native" or "introduced species", "provenances," etc., which were fully clarified at previous consultations.

Suffice to recall that, in most cases, species and provenance selection programmes have an economic purpose: the improvement of forest products in both quantity and quality. There are many examples of spectacular successes, but failures have also been recorded — sometimes on a large scale when the basic experimentation has been wanting.

One should also think of objectives less connected with the production of timber, such as selecting species or provenances for diversifying the forest flora, with the intention, for example, of protecting or establishing recreation forests. These concerns are, in fact, receiving increasing attention in a number of countries.

This type of selection constitutes the first selection to be made in any programme of genetic improvement. It consists of selecting from among the existing wild material, either within natural stands or in plantations, on the basis of inter- and intra-specific variability.

At first sight, this type of selection might appear to be less advanced than that which is based on individual variation, but in most cases it proves to be absolutely indispensable. We shall present a few of the arguments supporting this view.

The selection of species and provenances often constitutes an absolute prerequisite to any programme of individual selection. In fact, there is reason to doubt the effectiveness of a breeding programme based on parent stock chosen from a population (species, provenance) that is itself genetically inferior. Moreover, it is impossible to ascertain the best provenance of the best species for all sites in the world, but we can state that for several large reforestation zones it has been possible to identify, for several forest species, a certain number of populations of unquestionable genetic superiority (for example, for the species: *Pseudotsuga menziesii*, *Picea abies*, *Eucalyptus camaldulensis*, *Cupressus lusitanica*, etc.).

Sometimes the provenance selection programme makes it possible to go further and to estimate certain genetic parameters (and their intraspecific variation), such as the heritability or genetic correlation of the main characters, and this again helps to facilitate procedures during the subsequent stages of genetic improvement. In order to attain these objectives, it is necessary for the provenances to be represented by a certain number of descendants kept separate and clearly identified within the experimental plots.

If suitably conceived, a species and

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FIELD TRIALS IN SOUTHEAST ASIA
*looking for genetic variation*

provenance selection programme can supply information leading to interesting results of a fundamental nature on the following points, among others:

- Requirements of the species
- Laws of variation, in particular, explanation of genetic variation resulting from the selection pressure exerted by variations in environmental factors
- Genotype-environment interactions
- Evolution of the species, effect of selection pressure, and so on

Forest species (wild, perennial, wide-ranging) constitute excellent material for genecological studies.

The transfer of species leads to the creation of new populations (land races) thanks to the effect of selection pressure in the zones where they are introduced. It is already known that certain of these land races constitute excellent sources of seed for the region concerned (Douglas fir in Europe, *Cupressus lusitanica* in Africa, etc.). These "new gene pools" often deserve to be conserved and multiplied.

Nevertheless, experience shows that land races are not always the best. Thus, teak introduced into West Africa several generations ago is proving to be inferior to certain provenances from the species' natural range.

There is no doubt that the essential objective of species and provenance selection is to enable silviculturists to achieve an appreciable improvement in wood production.

A list of the successes obtained would be very long. The potential profit to be gained from the utilization of good provenances of interesting new species is considerable; it is quite feasible to aim at a doubling of production by this means. It should be noted, however, that enormous advances still have to be made.

Field trials, that is, establishment of comparative trial plots replicated on a number of sites, still seem to constitute a really indispensable experimental tool. The trial plots are installed in the middle of the reforestation areas concerned; they make it possible to compare genetic variation with ecological variation, which means that the greater the number of sites involved, the more effectual are the trials.

In addition to field trials, recourse can also be made to such new techniques as the use of biochemical criteria in setting up varietal tests or demonstrating the laws of intra-specific variation. Progress in this direction has been registered recently for species such as *Pinus sylvestris*, *Pinus nigra*, *Picea abies*, *Pinus pinaster*, through the analysis of enzymatic systems or terpenes. But despite the attraction and interest of these new methodologies, it would be imprudent to abandon field trials. In the present state of our knowledge, these are the only tests able to meet the specific requirements of forest trees, in view of their longevity and of the fluctuations in environmental conditions over the years that characterize many stations.

The criteria taken into account concern mainly the growth and shape of the trees of the various species or provenances tested. It is indispensable to enlarge the list of these criteria, by examining more particularly the quality of the wood, as well as any characteristic helping to explain the

behaviour and adaptation of the plant material studied. The list could include both phenological observations and analyses of pests or parasitic fungi.

One should not limit oneself, in fact, to noting the differences between provenances and species; an effort should be made to try and explain them (laws of variability), thus making it possible at a later stage to reduce the number of plots and in particular the number of provenances to be included in comparative field plots.

It should be noted that some of the more recent projects entail a very large number of provenances (up to one thousand), whence the necessity of using experimental plans with very small unit plots (including some with only one tree). The management and analysis of these designs could very rapidly pose problems which should be examined very carefully.

Finally, it should be pointed out that the idea of provenance has so far been applied essentially to social species. It should now be extended to species scattered throughout mixtures of other species. This problem regards many tropical species as much as some valuable species from the temperate regions.

The main stages in a species or provenance selection project are known. They are recalled briefly below.

Up to the 1960s, one of the major obstacles to the development of research programmes lay in the impossibility of obtaining reproduction material (seeds, cuttings) collected from natural or man-made forests suitably checked by sampling. For too long these studies were carried out using seeds obtained from botanical collections, or even of unknown provenance.

We have seen that over the last 10 years or so, enormous progress has been made in this field, in particular thanks to the organization of cooperative projects. In some cases, the research organizations concerned have to devote a considerable part of their resources to setting up the field trials with the numerous batches of seeds already collected.

However, two new types of requirements are appearing:

- The first results of the trials make it possible to identify the good

ARAB WOMEN TENDING AN EXPERIMENTAL DRY-LAND NURSERY

*breeding to suit the environment*

provenance regions, whence the desire to obtain new batches of seeds on the basis of more intensive selection in these favoured zones.

- Some countries wish to enlarge the list of species to be taken into consideration, including in particular tropical hardwoods of potential interest and species utilizable in arid and semi-arid regions. In the latter case, the aim is not always the production of wood: the provision of fodder and protection (including protection against wind) may have priority. A new list of species has recently been drawn up by the FAO Panel of Experts on Forest Gene Resources.

The many experimental plots (past and future) set up using material collected within the framework of international efforts are or should be analysed in a cooperative manner. This entails an effort of coordination at all stages:

- Establishment of experimental designs which are, if not identical, at least comparable with each other in the various zones or countries.

- Development and utilization of identical procedures for measurement and observation. A particular effort should be devoted to the methodology of observations on phenological stages, pest and disease damage, and measurements of wood quality.

- Establishment of coordinated timetables for measurements and observations.

- Utilization of modern means of data processing, at least at regional level.

It is recognized that this way of proceeding makes it possible to improve considerably the effectiveness of the experiments set up, which are usually very expensive.

In addition to the possibility of checking the results of each experiment against those obtained in all the others, this method also has the advantage of making it possible to estimate the effects of the interaction between genotype and environment and to identify " plastic " populations, i.e., those adaptable to a large variety of ecological situations.

In addition, such coordinated action also has the great merit of enabling countries or regions with limited research, infrastructures or equipment to benefit from the resources available and the experience acquired in other countries.

Recent examples have demonstrated the effectiveness of the assistance that can be provided through the implementation of programmes of this kind.

Finally, these examples (*Picea sitchensis* project, *Eucalyptus camaldulensis*, tropical pines, etc.) have shown that the undertaking is possible when a certain number of conditions are fulfilled. Two of these seem essential:

- People or teams must be found who are able to get the project moving. In some cases this is a fairly demanding task, calling for everything from field visits to discussions with those responsible for the project at national level.

- The responsible national personnel cooperating in the projects must accept a certain degree of discipline and follow the rules of the game proposed by the project leaders.

A rapidly increasing mass of reference material is available in this field of research, to the extent that national bodies which do not possess specialized documentation services may experience a certain amount of difficulty in selecting the most useful information.

At the level of each international project, the leaders are able to facilitate transmission of the results from the various trials.

In countries where there are a considerable number of programmes for species and provenance trials and conservation plantations, it is suggested that simple catalogues be prepared on the work done and the results achieved, for exchange between specialists.

Finally, at world level, a publication such as *Forest Genetic Resources Information*, edited by FAO, constitutes an interesting initiative for diffusing the most impressive results of the main programmes.

We have already emphasized the importance of the practical repercussions of species and provenance selection programmes.

It is still necessary, however, for silviculturists to be able to find on the market reproductive material selection through experimentation. Despite certain recent advances (OECD Scheme), the situation does not appear to be very satisfactory.

In fact, the system of collection and control is the responsibility of each individual country and the first concern of the national authorities is with internal supplies. Any external customer encounters difficulties in obtaining commercial quantities of seeds when specific sources are required. The OECD Scheme is, by definition, strictly voluntary and cannot be coercive.

In order to resolve this problem, at least in the future, it is suggested that networks of plantations for the conservation of provenances be set up on a regional basis, with the following three main roles:

- Supplying the region with reproduction material.

- Providing a source of individual selection for future improvement programmes.

- Conserving gene pools.

This action could be undertaken or pursued in conjunction with those to which reference is made within the framework of session 1, " Exploration, utilization and conservation of gene resources ", and in conformity with the recommendations of the FAO Panel of Experts on Forest Gene Resources.

The recent development of techniques of floral induction could reduce the delays encountered in obtaining seeds.

Collaboration at the international level may prove to be necessary here.

Great advances in species and provenance selection have been made during recent years, in particular thanks to the development of international cooperation.

These advances will result in an improvement in the effectiveness of reforestation work, mainly from the economic point of view. It is to be hoped that these research programmes will be conducted and analysed in such a way as to cover the greatest number of countries and supply the maximum amount of information useful for forestry.

# Population improvement and hybridization

**D.P. Fowler**

Forest tree breeding was conceived in the latter part of the 19th century, born in the early 1900s, and developed into adolescence in the 1950s. It is now, as we enter the final quarter of the twentieth century, approaching maturity. The first World Consultation on Forest Tree Breeding, held in Sweden, could be characterized as having been hopeful; the second, held in the United States, was full of promises and predictions; now, at the Third Consultation, we can look back and see that the hopes, the promises, and the predictions of the earlier Consultations are being fulfilled. The number of active tree breeders has increased from a few score in the early 1950s to several hundred (Toda, 1974), and tree breeding has become a science. Genetically improved seeds and seedlings now provide a small, but significant, contribution to several afforestation programmes throughout the world.

Although severall breeding programmes are reaching maturity and in some instances work on second generation programmes has begun (Weir and Zobel, 1975), there are many more that are still in their infancy and some that are yet in their conceptual phase. Most of the relatively advanced breeding programmes deal with coniferous species, especially *Pinus*, and it is from these advanced programmes that much of our present information is derived. Only recently has a significant portion of our resources been directed to improvement of non-coniferous species. Angiosperms, especially the tropical ones, are now beginning to receive attention.

The experience and information gained from the more advanced breeding programmes will undoubtedly prove useful for the development of new programmes with "genetically unknown" species. Just how much of the information from programmes with coniferous species will be directly applicable to other genera and species is a rather moot question.

An understanding of reproductive biology and natural breeding systems

THREE-YEAR-OLD CANDIDATE FOR SECOND-GENERATION SELECTION
*creating an elite*

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is important for the development of breeding strategies and for determining the actual genetic gain attained in improvement programmes. Eldridge (1977) emphasizes the importance of obtaining this information at an early stage in the development of improvement programmes. It is not enough to accept and utilize the strategies of other programmes for the improvement of new, genetically unknown species. For example, a strategy that works well for a generally outbreeding, highly variable species would be quite inappropriate for a species containing little variation or for a species in which selfing is an important means of reproduction.

**Conifers.** Over the past decades much has been learned about the reproductive biology and breeding systems of several important coniferous species. The reproductive biology of conifers is reasonably simple. They are essentially diploid, monoecious, and wind-pollinated, and have evolved only a few simple, but effective, mechanisms to control inbreeding (Koski, 1973). These mechanisms include spatial separation of male and female strobili and, in a few species, phenological differences in receptivity and pollen shedding. Self-incompatibility in conifers is dependent on the frequency of recessive lethal (or semi-lethal) genes within the individual tree genome and not upon highly sophisticated sterility gene systems (Hadders and Koski, 1975) which have evolved in many non-coniferous plants. Estimates of natural selfing for different conifers are surprisingly similar considering the large number of species and the varied conditions under which they grow. Although most coniferous species exhibit considerable tree-to-tree variation in self-compatibility, natural selfing is generally less than 10% under stand or plantation conditions.

The level of inbreeding (selfing, plus crossing of related trees) that occurs under natural conditions is still not well understood. Intuitively, it is widely accepted that within stands relationships do exist (Ledig, 1974), but it has only been recently that attempts have been made to quantify these relationships (Sakai *et al.*, 1970; Sakai and Miyazaki, 1972; Tigerstedt, 1973; Coles and Fowler, 1976). Snyder (pers. comm., 1973) found that crossing neighbouring trees (less than 300 m apart) resulted in 2-14% reduction in seed and seedling characters. Coles and Fowler (1976) reported relationship coefficients of r = .30 and .23 for two stands of *Picea glauca*. Morgenstern (1972) reported relationship coefficients of r = .16 and .06 for *Picea mariana* growing in southern and northern Ontario, respectively.

The relationship among trees within populations has important implications for choosing the most effective selection methods (Ledig, 1974) and for determining actual genetic gain attained from a phenotypic selection programme. Several papers presented during this session of the Consultation have indicated strategy changes in which selection intensity will be reduced in the "wild" so that larger numbers of trees can be included in the programmes (Kellison and Dinus, 1977; Pederick and Griffin, 1977). Under these conditions, especially for species of limited natural range, an understanding of within-population relationships increases in importance.

A portion of the gain attained from clonal seed orchards may well be attributed to reduced inbreeding in orchards. The substantial gain in yield from unrogued seed orchards of loblolly pine over that of commercial checks (Kellison and Dinus, 1977) may include a fortuitous gain derived from reduced inbreeding compared to the level of inbreeding in natural stands, while the smaller gain reported for plantation origin Monterey pine in Australia (Pederick and Griffin, 1977) would not. One might argue that a gain is a gain, and in a sense this is true. On the other hand, if relationship coefficients had been known and taken into account, an even more effective breeding strategy might have been followed.

**Non-coniferous species.** With the exception of a few well-studied genera, e.g., *Populus*, *Tectona*, and *Eucalyptus*, information on the reproductive biology and breeding systems of angiosperms is considerably more limited than it is for conifers. What is known indicates that both these factors will be complex. Improvement of angiosperms will confront breeders with problems unknown by conifer breeders. Angiosperm breeders must contend with problems involving ploidy (Kim *et al.*, 1977; Dancik, 1977), complex pollination mechanisms, highly evolved and more variable systems to control inbreeding (Tufuor, 1977), and quite possibly very different problems involving population structure.

The importance of basic information for the development of appropriate breeding strategies is well illustrated by Eldridge (1977), Wyk (1977), and Venkatesh and Vakshasya (1977) for *Eucalyptus*; Badran and El-Lakany (1977) for *Casuarina*; Wang (1977) for *Pinus ponderosa*; Toda (1977) for *Larix leptolepis*; and Tufuor (1977) for *Terminalia ivorensis*. It is imperative that a reasonable portion of the resources available to any new breeding programme involving a genetically unknown species be devoted to providing basic information on reproductive biology and breeding systems. This information will be essential for the development of optimal breeding strategies.

### Individual tree selection

Following species trials and provenance trials most breeding programmes have concentrated on mass selection of phenotypically superior trees on the assumption that these trees are "above average" genetically. Working criteria for selection have been developed and are being utilized in many programmes, but these criteria differ greatly by species and by the objectives of specific programmes. In the more advanced breeding programmes, information is now available on the genetic control of most important attributes and it has been possible to modify selection criteria in some instances (Fletcher and Faulkner, 1972). Growth attributes continue to be important selection criteria, but emphasis has shifted in several programmes to selection for the more highly heritable features such as branch and stem form (Pederick and Griffin, 1977) and for disease resistance (Kellison and Dinus, 1977). Greater reliance is being placed on progeny testing for the improvement of growth and yield.

IRANIAN FORESTRY STUDENTS IN TRAINING
*stressing the practical*

Comparison tree selection as developed by the Zobel school, or some modification of this system is most widely used. However, base-line selection (Ledig, 1974) is gaining in popularity where the desired attributes are known to be under reasonable genetic control or where strong intra-population relationships are known or suspected. For several species, the rigorous selection criteria used to attain a large selection differential have been softened so that more good trees (rather than a few super trees) can be utilized. This shift to larger numbers has developed because of the relatively low heritability of growth attributes for "wild" selection (Fletcher and Faulkner, 1972), the need to maintain a broad genetic base to make possible a reasonable level improvement in the second and subsequent generation of breeding (Pederick and Griffin, 1977), and to allow for selection for attributes such as disease resistance (Kellison and Dinus, 1977; Palmberg, 1977) which may not have had high priority in the original selection criteria.

## Testing

Progeny testing is an integral part of most improvement programmes. The tests are used as a basis for assessing breeding values and roguing clonal seed orchards, for the development of seedling seed orchards and as a means to provide materials for subsequent improvement efforts using inter- and intra-family selection. These tests can take many forms depending on species, improvement objectives, strategies, and are discussed in detail by Nanson (1974) and Wright (1976). Burdon and Shelbourne (1974) discuss the use of vegetative propagules for obtaining genetic information.

Clonal selection and testing have in the past been restricted to genera such as *Populus* and *Salix* which root readily from stem cuttings and exhibit a minimum of topophytic effects. Recent advances in vegetative propagation methods, including techniques for eliminating or reducing topophytic effects, improve the possibilities of clonal propagation as a mass production method (Libby, 1974). The possibility that tissue culture will provide even better means of mass producing clones is high (Brown, 1976; Durzan and Campbell, 1974). Several large-scale programmes involving "difficult-to-root" species are presently under way, e.g., *Picea abies* (Kleinschmit, 1974; Lepistö, 1974), *Pinus radiata* (Shelbourne and Thulin, 1974).

Breeding strategies have been re-

uated or modified on the strength of information obtained from progeny tests. For example:

**A** – Dominance variance is considerably greater than previously anticipated for the southern pines (Dorman and Zobel, 1973; Dorman and Squillace, 1974) and for *Pinus radiata* (Pederick and Griffin, 1977). Different breeding strategies such as the use of bi-clonal orchards or controlled pollinations will be required to capitalize on this variation.

**B** – Genotype × environment interactions, although often evident (Toda, 1977; Wang, 1977), do not pose insurmountable problems (Shelbourne, 1972). Most improvement programmes breed for widely adapted types rather than for types best adapted to specific environments (Kellison and Dinus, 1977).

**C** – Correlations between traits have generally been found to be favourable or not strongly expressed (Barnes, 1977; Kellison and Dinus, 1977). An exception to this is a positive relationship between growth and gummosis in *Acacia mearnsii* (Nixon, 1977). The multi-trait criteria for selection used in most improvement programmes are satisfactory.

**D** – Trees with exceptionally good general combining ability have been identified in some programmes (Weir and Zobel, 1975) and support the need to utilize a pedigree breeding scheme if inbreeding is to be maintained at low levels in future generations.

**E** – Juvenile-mature correlations have generally been reasonably strong and provide encouragement for the development of early selection procedures.

### Seed orchards

Although most current planting programmes are still based on seed obtained from wild unselected populations, seed orchards are beginning to make a contribution to afforestation efforts with several species. Faulkner (1975) provides a good up-to-date review of all aspects and problems of seed orchards, including design, establishment, management, and protection. Seed orchards have been established in more than 40 countries for the production of seeds of approximately 50 different species (Feilberg and Segaard, 1975). First generation orchards associated with some of the more advanced breeding programmes are producing significant quantities of seed. For example, *Pinus radiata* orchards in Australasia provide 15-60% of seed requirements (Pederick and Griffin, 1977), and in the United States all *P. elliottii* and *P. taeda* seed will be available from orchards by 1990 (Kellison and Dinus, 1977). Dvorak (1977) reports that all *Pinus caribaea* seeds used in Fiji will come from orchards by 1986.

Grafted clonal orchards are by far the most widely used at the present time. Stock-scion graft incompatibility has proved to be a serious, but not insurmountable, problem with several species (Hong, 1975). Several techniques, including the use of rooted cuttings rather than grafts and selection of compatible stock have been used to successfully combat incompatibility. Seedling seed orchards which combine progeny testing and seed production are being more widely used, especially for precocious species or for species that are difficult to propagate vegetatively. Wright (1976) provides a detailed discussion of the advantages and disadvantages of seedling and clonal orchards.

**A reasonable portion of the resources available to a breeding programme involving a genetically unknown species must be devoted to providing basic information on reproductive biology and breeding systems, essential for developing optimal breeding strategies.**

Most seed orchards have been designed to accommodate wind-pollinated, relatively self-incompatible coniferous species. The suitability of these types of orchards for insect-pollinated or highly self-fertile species is questionable. Wyk (1977) suggests the planting of ramets of *Eucalyptus grandis* in hedge rows so that their branches will intermingle, or planting 2-3 ramets of different clones in the same planting site, as a more appropriate means of seed production for this species.

The conventional multi-clonal seed orchard is designed primarily to capture additive genetic variance. It has become evident that non-additive variance can also be important in some species (Pederick and Griffin, 1977; Kellison and Dinus, 1977) and that unique orchard designs will be required if non-additive variance is to be utilized, i.e., bi-clonal orchards, non-random distribution of clones in orchards or selective mass pollination (Pederick and Griffin, 1977). Selective mass pollination, especially during the early production years, may be required to combat background pollen or to reduce selfing, even in conventional orchards (Denison and Franklin, 1975; Furukoshi, 1977).

### Genetic gain

During the past several years methods for predicting genetic gain in tree species have developed a high degree of sophistication (Shelbourne, 1969, 1971; Namkoong, 1972; Wright, 1976) and estimates of gains for various selection and breeding strategies abound in the current literature. It is beyond the scope of this report to attempt more than a cursory review of the subject. It is enough to state that estimates have been obtained for many traits for most important species and that in most cases these estimates indicate that economically worthwhile gains are attainable. In fact in a number of improvement programmes, offspring from first-generation seed orchards have been tested against "commercial" checks to determine realized gains.

Rogued, first-generation orchards of *Pinus taeda* and *P. elliottii* have produced stock which, in operational plantings, is 10% to 20% greater in volume than commercial checks at six years (Weir and Zobel, 1975). Improved stock from first-generation orchards from five improvement pro-

A TEN-YEAR-OLD *Pinus taeda* ORCHARD IN THE UNITED STATES
*quality also requires quantity*

grammes in Australia and New Zealand is —10% to 53% (X = 8-10%) greater in volume than commercial checks (Pederick and Griffin, 1977; Eldridge *et al.*, 1977). Barnes (1977) found that polycross progenies of *P. patula* in Rhodesia produced volume increases of 17% at 5 years and 37% at 8 years over commercial checks and reported that comparable gains were obtained from *P. elliottii* and *P. taeda* in South Africa.

Of interest is the fact that all the above programmes were based on multi-trait selection schemes and that comparable gains in other traits, except for disease resistance (Kellison and Dinus, 1977), were also attained. The results from these tests are very encouraging in that the predicted gains are not out of line with realized gains.

### Advance generation breeding

Strategies for the development of long-term genetic improvement programmes have been discussed in detail by Burdon and Shelbourne (1971), Libby (1973), Namkoong (1974), and Weir and Zobel (1975). Although the proposed strategies differ quite markedly, they all recognize the need to separate the short-term seed production function from the long-term goal of developing and maintaining broad-based genetic populations for future advances in tree improvement. The proposed strategies also allow for the infusion of new genetic ma-

terial into the breeding populations to broaden the genetic base, and thereby reduce inbreeding. Controlled crossing and complete pedigree records are essential if the greatest gains are to be achieved and inbreeding is to be avoided in advance generations (Zobel *et al.*, 1972; Weir and Zobel, 1975).

It is recognized that a unified effort between countries or regions, working in the improvement of the same species, and the sharing of breeding materials offer many long-term advantages to a number of breeding programmes (Pederick and Griffin, 1977; Barnes, 1977; Muniswami, 1977; Dyson, 1977).

## Hybridization

Although species hybridization has proved to be a viable improvement strategy for some genera, it is by no means the tree improvement panacea it was once considered to be. Brown (1972) provides a detailed review of the role of inter-specific hybridization in forest tree breeding. The role of species and provenance hybridization is also dealt with in detail in the proceedings of a symposium on that subject (Fowler and Yeatman, Eds., 1973). Brown (1972) concludes that hybridization is rarely a useful tool in tree improvement, which agrees with the general conclusion of the symposium.

The reasons that hybridization has failed to fulfil its promised goal are many — the most important being that there are usually better or more economical means of achieving the same goals. Heterosis or hybrid vigour in species and provenance hybrids is the exception rather than the rule (heterosis as used here is synonymous to Dobzhansky's (1964) "luxuriance" and does not imply greater fitness in the genetic sense). Genetic differentiation between species as well as between widely separated populations of the same species has usually arisen by evolutionary adaptation to local conditions (Falconer, 1975). The crossing of these species or populations disrupts the highly evolved, but different, adaptive systems and often results in hybrids that are less fit than either parent species. This reduced fitness is often expressed in reduced seed set, increased frequency of abnormal or inferior seedlings, and in reduced vigour.

A further point that often militates against hybridization as a viable alternative to other improvement approaches is the greater complexity of hybrid breeding strategies (Shelbourne, 1969) and the lower predictability of results as a result of a paucity of tested genetic theory relating to species hybrids (Stuber, 1970; Lester, 1973). The existence of strong maternal effects, as illustrated by the differences between reciprocal crosses of *Eucalyptus camaldulensis* and *E. tereticornis* (Venkatesh and Sharma, 1977), may be more pronounced in species hybrids.

Hybridization does create new gene combinations, some of which may be superior to those available within either parent species. Where these can be captured and economically utilized, hybridization offers a viable alternative to other improvement schemes. Vegetative propagation is one means of capturing exceptional gene combinations and it is in those tree genera which can be easily propagated vegetatively that species hybridization has had, and will have, its greatest impact. Species hybridization has proved to be a very successful approach to the improvement of *Populus* and *Salix* species (Zsuffa 1973). Both these genera contain many "crossable" species, most of which can be propagated vegetatively. Inter-specific hybridization does appear to hold considerable promise for *Eucalyptus* which has generally been considered to be "difficult to root." The successful rejuvenation of *Eucalyptus* hybrids forms strong sprouts and the direct use of these on a large scale in the Congo (Chaperon, 1977a, 1977b; Chaperon and Guillet, 1977) is most encouraging.

In recent years there has been a renewed interest in the use of vegetative propagation as a mass production technique with "difficult-to-root" species. If the problems of tree ageing can be overcome, as suggested by Libby (1974) and Kleinschmit (1977) and if more effective means of mass propagation, e.g. tissue culture, can be developed, hybridization can play an important role in the improvement of several other genera.

Well-documented examples of heterosis include:

*Larix leptolepis* × *L. decidua* (several, see Brown, 1972)

*Pinus elliottii* × *P. caribaea* (Nikles *et al.*, 1977)

*Plantanus orientalis* × *P. occidentalis* (Santamour, 1970)

*Populus* hybrids (Zsuffa, 1973)

*Salix* hybrids (Barrett and Rial Alberti, 1972)

*Pinus nigra* × *P. densiflora* (Wright *et al.*, 1969; Vidakovic, 1974)

*Eucalyptus* hybrids (Chaperon, 1977)

## A useful tool

Species hybridization has proved to be a useful tool for the combining of specific attributes such as disease resistance or cold hardiness with growth attributes of another species. Examples where hybridization is being used for the following purposes are:

### Resistance to disease

*Castania dentata* × *C. molissima* (Diller and Clapper, 1969)

*Pinus strobus* × *P. griffithii* (Zsuffa, 1975)

*Ulmus pumila* × *U. japonica* (Lester, 1973)

*Larix leptolepis* × *L. decidua* (Brown, 1972)

### Increased cold hardiness

*Fraxinus excelsior* × *F. americana* (Rohmeder, 1964)

*Pinus rigida* × *P. taeda* (Hyun, 1969)

*Pinus attenuata* × *P. radiata* (Griffin and Conkle, 1967)

Species hybridization has also been used successfully to determine phylogenetic relationships within tree genera (Critchfield, 1967; Wright, 1955).

Despite the successful use of species hybridization to bring together specific high-value attributes and some modest success in producing heterotic progenies, it must be concluded that intra-specific methods are more promising for the genetic improvement of most trees.

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References are at the back of the magazine following the last article.

# Primary considerations: multiplication and genetic diversity

**Hans M. Heybroek**

PROGENY TESTING IN SCANDINAVIA
*a basic step in tree breeding*

The first task of a forest breeder is to identify or produce superior genotypes of forest trees, be it through selection, provenance tests, introductions, test crosses or hybridization. In most cases, this does not lead immediately to products ready for use by the foresters. Before improved genotypes can be used on a large scale, it is necessary that problems be solved about their multiplication and about the required degree of genetic diversity in the planting material. Though these questions are not in all cases reckoned to be the immediate task of the forest tree breeder, he can never neglect them as they may have serious implications for his breeding strategy.

## Seed orchards

Seed orchards are one of the main tools of the forest tree breeder. Through them, he hopes to provide the foresters with quantities of seed of an improved genotype for large-scale use in afforestation and reforestation.

Seed orchards require a large investment in land and labour, in planning, establishing and maintenance. The expectation that they really will produce the desired quantities and qualities of seed is at the basis of these investments and often even at the basis of the major decision of starting a breeding programme.

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Many questions about seed orchards have now been answered in an excellent handbook, the outcome of the activities of the Working Party on Seed Orchards of the IUFRO (Faulkner, 1975). It should be stressed that many seed orchards are beginning to fulfil their aims. Others, however, present difficulties. This has recently been summed up as follows:

It would appear that the yield of seed orchards is not living up to expectations. The most common (problem) was that many families are failing to produce an adequate number of male or female flowers. The actual seed yield is then produced by relatively few individuals, thus defeating the orchard design for a broad genetic base. Self-fertilization may become a dominant feature of such orchards. Even when flowering appears sufficient, there still occurs an extremely high abortion rate. Even when the cones mature, the ratio of full to potential seeds per cone may be extremely low. We need to re-evaluate our concepts and approaches if we are to realize the maximum seed yield and quality of "tree improvement effort" (Krugman, 1976; for a further discussion see Sweet and Krugman, 1977).

In the humid tropics, introduced pines but also native species may offer big and unexpected problems for propagation by seed through irregular flowering, poor pollination, flower abortion and low seed set. More research on these aspects is needed (Sheikh Ibrahim, 1977; Tufuor, 1977).

A fundamental problem of the seed orchard may further lie in the fact that the seed orchard aims at a high seed production whereas the seed produced should give rise to trees with a fast vegetative growth. These two goals may conflict where there is an inherent antagonism in a tree between seed production and vegetative growth. Such an antagonism is very well-known in apple trees and described for several forest trees (Heybroek and Visser, 1976; Teich, 1975; Heybroek, 1974). It may even be that the earlier and heavier flowering populations represent less desirable biotypes (Delaunay, 1977; Heybroek, 1974).

For that reason, genetic means of improving the seed production of seed orchards, for example by selecting heavily seed-producing clones or by selecting those clones that start flowering in a seed orchard relatively soon, should be considered to be not without risk. From this point of view, also the fact that in some seed orchards the bulk of the seed is produced by a few precocious and heavy-seeding clones should be viewed with suspicion. The resulting seedlings might similarly be early and heavy flowering and have an early culmination of growth.

This means that more attention should be given to non-genetic and even to quite artificial means of increasing the production of a seed orchard. For instance, there is promise in locating the orchard in an area with a climate that is conducive to flowering and seed production. This may be effective (Sweet, 1975; Werner, 1975; Gansel, 1973) but it often requires much international cooperation. Unfortunately, our knowledge on the ecophysiology of flowering is often insufficient for choosing locations with optimal conditions. Placing the entire seed orchard in a greenhouse (Koski, 1975) or treating the constituent trees every second or third year in a greenhouse (R.C.B. Johnstone, pers. comm.) may provide a solution in some cases. The influence of soil types, pruning, girdling, irrigating and fertilizing on seed production has been reviewed by Sweet (1975), Werner (1975) and Schmidtling (1975).

**Genetic diversity is the only defence we have against the many unknown dangers which plague trees throughout their long lives.**

Manageable methods to control flowering in the seed orchard may ultimately result from an important recent scientific breakthrough showing the big role of certain gibberellic acids in the flower induction of the Pinaceae (Pharis *et al.*, 1976; Ross and Pharis, 1976).

In looking for parallels in the apple orchard (which undoubtedly was the model when the term "seed orchard" was coined), it is striking to see how much modern fruit growing depends on special rootstocks to regulate fruit production. It is hard to believe that what applies to apple trees would be entirely unapplicable to all forest trees. More likely, the lead that apple culture has over us is based on ages of practical experience and on much research. Research aimed at finding precocious and dwarfing rootstocks for important forest tree species like Norway spruce seems feasible and highly desirable. There are indications of the existence of such types (Anon., 1975; Dyson, 1975). The dominant role which has been played by a single research station in the development of the various apple rootstocks may show that a concentrated research effort, perhaps in international cooperation, is needed to develop a range of rootstock types fit for the establishment of fast- and high-yielding seed orchards.

Once the seed orchard produces sufficient female flowers, the seed production may be limited by insufficient pollination. Evidence accumulates that supplemental artificial pollination can increase production (Denison and Franklin, 1975; Hadders, 1977) as well as reduce the high proportion of selfing that occurs in some seed orchards (Furukoshi, 1977), but there remains a need to develop good methods of mass pollination. Depending entirely on artificial pollination, Sweet and Krugman (1977) have designed a novel type of seed orchard for *Pinus radiata*. In these orchards, male flowering is prevented by clipping the cone-bearing clones at certain intervals, so that they form hedges. This also keeps female flowers and cones at a workable height.

### Vegetative propagation

Until recently large-scale vegetative propagation of forest trees has been limited to some species of *Populus* and *Salix* and to some clones of *Cryptomeria japonica* and *Ulmus*. As these are relatively easy to root, breeding can proceed from crossing, via selec-

tion and clonal tests, to large-scale clonal planting (except for *Cryptomeria*, see Toda, 1974).

The majority of forest tree species does not allow cheap large-scale vegetative propagation. Though most trees can be propagated by grafting, this is too expensive for use in forestry. Grafting incompatibility sometimes adds another difficulty.

### Mass propagation

Modern research and technology, however, have developed feasible methods for mass progagation by cuttings of a few other important forest trees: Norway spruce, radiata pine and in Africa *Triplochiton scleroxylon*, Eucalyptus and others (Longman *et. al.*, 1977; Chaperon and Quillet, 1977). This has offered a multitude of new interesting possibilities and problems (Kleinschmit, 1977). Fundamental to these developments is the recognition of the fact that all trees seem to have a juvenile stage during which they are easier to root from cuttings than later in the adult stage. In the species mentioned, cuttings of juvenile plants root easily enough for mass propagation.

This fact has many consequences.

In the absence of methods to rejuvenate a tree, clones must be made from young trees before these have proved their superiority. This stresses the value of family selection and necessitates the use of early tests. It requires methods to maintain the juvenile stage in some part of the basic material of the clones forever or at least for a much longer period than in the undisturbed seedling. It poses questions about any other differences that may exist between the juvenile and the adult stage, for example, to what extent fast growth of the ortet is found in the cuttings for which root development is a different process, and on the essence of the process of ageing (Zimmerman, 1976). It makes us wonder how much gene-environment interaction there is at the individual tree level in a population, and it stresses the need for genetic variation in planting stock (Kleinschmit, 1977). It may entail problems of certification. Kleinschmit (1977) has shown how a higher initial cost of the cuttings can be offset by a higher genetic gain or by the opportunity to plant at a wider spacing.

It offers, on the other hand, prospects for a much higher genetic gain than is possible with sexual propagation (Kleinschmit, 1977) and it circumvents all problems with seed orchards. It may also allow us to use rare provenance or species hybrids or other exceptional genotypes (Schreiner, 1966). If handled with care, it can increase rather than diminish genetic variation, and it can be built into a very flexible improvement programme. It may prepare us for the problems and potentials that will come with future methods to produce trees large-scale by tissue culture.

**Trees and forests are more to man than a source of wood. They are an environment and their perceptible qualities influence man's emotional and spiritual well-being.**

Breeding can easily lead to situations where the naturally occurring populations of a species with its wide genetic variation are replaced by much more uniform, " improved " materials over wider and wider areas. Similarly, a promising introduced species may be planted to cover whole provinces. While each extension of the area with such new materials may be expected to lead to a proportional increase in productivity, this may not come true. At more than one level and in several respects, genetic variation is a positive value and therefore it should be considered a breeding goal. Its neglect entails disadvantages as well as considerable risks. Genetic diversity generally is part of nature's strategy for the survival of populations.

Genetic diversity in the planting stock is an obvious and necessary precaution whenever a chance exists that the next generation of forest will be founded by natural seeding. To prevent inbreeding depression in the first generation and to minimize it in following generations, genetic diversity in the planting stock — that is, absence of relationship between components — is required. The amount of genetic diversity required can be computed; it is comparable to the amount of plus trees needed in a collection to be used for second-generation breeding.

### Genetic variation

Genetic diversity in the planting stock may prove to be very useful to the breeder later because it enables him to select and use outstanding individuals in the resulting stands, maybe also for some additional property that was not considered in the earlier breeding programme. In this way, genetic variation in the planting stock may contribute to gene conservation.

Four other reasons for cherishing genetic variation will be discussed in more detail, with an emphasis on the " why ", on the mechanisms that can make variation more desirable than uniformity. The popular theory on diversity-stability relationships, rightly criticized by Goodman (1975), will not be invoked.

Forests and other plantings of trees are more to man than a source of the commodity wood. They also form an environment to man, and as such their perceptible or visual quality can have a significant influence on his emotional and spiritual well-being. Especially in densely populated areas, this is one of the main functions of trees. This situation offers special problems and opportunities to the forest tree breeder (Koster, 1974; Townsend, 1977).

It should be realized that for amenity or landscape use plantings consisting of one clone may have a visual effect that is entirely different from the effect of a planting of seedlings of the same species (Heybroek, 1976). Clonal plantings are especially suited for situations where the need for a formal or monumental effect and for a strict preconceived pattern requires the geometric repetition of trees of exactly the same shape in rows or blocks, or where one wants to emphasize the " rational " aspect of a certain landscape. By their uniformity, even-aged trees of clonal stock emphasize their

occurrence as a group rather than as individuals. Where a relaxed, natural atmosphere is required, however, seedlings are at an advantage. Contrary to clones they stress the tree to tree variation, demonstrating the ever-present individual differences in shape, growth rate, pattern of branches and leaves, colour, density, flowering, leafing etc., which form a constant source of interest and job for the onlooker. The human eye loves and searches for variation and detail. It immediately notes damaged or missing trees in clonal plantings; in seedling plantings, each tree differs from its neighbours and gaps are less conspicuous. Clonal plantings, especially if even-aged, can bring an element of monotony to the landscape. The replacement of seedling trees by uniform clonal stock may result in a definite loss in the visual quality of a landscape.

Obviously, the amount of variability present differs between populations: there may be populations with too much and others with too little variation for certain purposes.

Variation at the species level is equally important. An extreme diversity of species is rarely the ideal, however. Ideally, a landscape should have a recognizable pattern or a theme on the one hand and plenty of variation and detail on the other hand: "variety within order." The preponderance of a certain species in an area can thus be right if it fits the pattern-aspect (compare Rapoport and Hawkes, 1970).

### Production

It seems astonishing that so few firm data exist on the differences in effect between genetic variation and uniformity in trees on production per unit of area. Model experiments with agricultural crops seem to lead to the conclusion that a mixture (of pure lines or species) produces, in general, at an intermediate level, that is, less than the better component and more than the poorer component when these are grown pure and under the same conditions.

There are indications, however, that the mixture can produce more than any of its components over a long series of years in case the weather during that period fluctuates sufficiently to make now this rather than that component the better producer. This can be explained by the phenomenon of compensation: if one of the components suffers a set-back (by forest, drought, parasites, etc.) early in the development of the mixture, another component may be able to use the vacant space. Thus the mixture will yield more than the arithmetic mean yield of the components.

What holds for weather may hold for site: on a highly heterogeneous site, a mixture may do better than any of its single components; each component will tend to dominate on the site it can utilize best. Depending on its composition, the mixture can thus be more flexible and better buffered against variations in time and space, in weather and site quality in its environment.

Especially in forest trees, which must live many seasons on sites that can be much more variable than those of agricultural crops, and often on sites that are not too well known, good mixtures of genotypes may have an advantage by being better buffered.

### Gene environment

In this view, gene-environment, or GE-interaction in the materials is a prerequisite for superiority in the mixture: only if the different genotypes react differently to different environments has a mixture a chance to be superior. GE-interaction at the individual tree level is what counts here and this can be measured with the help of clones (Matheson, 1977). It is largely independent of GE-interaction at the population level, which is the level usually studied (Goddard, 1977).

With regard to production, mixtures become even more interesting if and where overcompensation can be shown, that is, where the mixture produces more than any of its single components. In such cases, apparently, other mechanisms than GE-interaction are involved. A case of overcompensation has been reported for poplar by Tauer (1975). De Wit (1977) suggests such overcompensation may occur especially on very poor sites, not on the better sites.

The problem has similarities in silviculture where the pros and cons of mixed versus single-species forests are being discussed; in both fields, experimentation to determine the magnitude of the advantage is difficult.

### Unknown risks

Genetic diversity is the only defense we have against unknown dangers and risks, which play such a big role in forestry, due to the long lifespan of a tree. It certainly is not a perfect defense, it just is the only one we have. Rather than being a real defense, genetic diversity is a way to spread the risks.

These risks are of many kinds. A risk familiar to most tree breeders lies in the fact that we cannot test the new — and hopefully better — materials we produce over a full rotation and under all conditions. We often release new materials at a stage when they are "promising," which implies that their use contains the risk of disappointment at a future stage. Later in life, or when planted outside the testing area, they may show unexpected physiological weaknesses, susceptibilities to parasites, etc. (Toda, 1974). Similarly, the once-in-fifty-years' weather falls outside the normal testing period and thus constitutes an unknown risk. Because of these unknowns a breeder will often try to release different materials to spread the risks.

Basically the same holds for a much more grave and complicated problem, the danger of "new" diseases and insects. The examples of the introduction of chestnut blight and Dutch elm disease in North America and Europe, of *Marssonina brunnea* in Europe, of *Rhabdocline pseudotsugae* in Europe, of two poplar rust species in Australia and New Zealand and of *Phytophthora cinnamomi* in Western Australia are well-known. Others can be listed, and many more fungi seem just to be waiting for a lift to a new continent to make history in a similar way. For the purpose of this discussion, a genetically based increase in the pathogenicity of a parasite (Snow *et al.*, 1976; Gibbs *et al.*, 1975) falls in the same category of "new" diseases.

REFORESTING LEBANON WITH CEDARS
*part of a national "green plan"*

With regard to genetic variation within the species, the impacts of the mentioned epidemics show clear differences. It seems important to recall that the full natural variation of the species did not save the American chestnut from a virtually complete eradication by the chestnut blight. Similarly, in large parts of the species area, the American elm as a tree seems headed for the same fate due to Dutch elm disease. Both are native, not introduced, tree species. This shows that natural variation is not a magic cure for all problems.

In other cases, a different picture emerges. While the first impact of the importation of *Cronartium ribicola* on the western white pine *Pinus monticola* was disastrous, the species apparently has sufficient genes for resistance in its gene pool to come back as a more or less resistant species in few generations, a process that can be accelerated by the breeder (Hoff *et al.*, 1976). Poplar culture in Italy was hit hard after the advent of *Marssonina brunnea* because of the preponderance of the clone I 214 that just happened to be very susceptible; in the Netherlands on the other hand, more clones were cultured widely, of which only one proved highly susceptible. Additional genetic variation that was accumulated in an active breeding programme allowed the speedy release of two highly resistant clones, so that the new disease resulted mainly in a shift in the assortment of clones used. In the case of *Rhabdocline pseudotsugae* in Western Europe, only a fraction of the varied host population was attacked severely; after the disappearance of that part of the population, the disease became of minor importance.

These examples may suffice to show that the impact of a "new" disease

on a species can vary widely. How big a part of the species will turn out to be susceptible under the local conditions and to what degree is mostly unpredictable. It is clear that the presence of genetic variation in the host species can play a major role in preventing catastrophic results and saving the culture of a species even after initial losses.

Yet because these dangers are really unknown and unpredictable, it is impossible to say *how much* genetic variation should be needed to reduce risks to some acceptable level. One can only strive to include as much genetic variation in the planting stock as possible, and decide in each case how much one is prepared to sacrifice for it in the way of cost or productivity.

Genetic variation at the species level is a very obvious and generally reliable line of defense against the dangers concerned. It is risky to rely on a single species over large areas; diversification seems advisable.

### Mutual protection

The multiline in small grains as described by Browning and Frey (1969) is a highly refined and sophisticated cultivar, consisting of a mixture of pure lines being practically identical as far as most properties are concerned but differing in resistance to the different races of the rust. Each line has a resistance to a certain set of races, none is resistant to all. Lines with different resistances are mixed more or less in proportion to the share each rust race had in the spore cloud last season. The resulting multiline cultivar is not free from rust, but it never suffers real damage by it. Equally important, it aims at stabilizing the rust population in its composition over the years, preventing the development of new races. It is a safe way to employ "vertical" or specific resistance.

This goes to show that this sort of multiline is a defense against an exactly known and defined parasite. Genetic variation is carefully dosed against that single enemy; for the rest, the cultivar is homogeneous. It is an inspiring example because it shows how genetic variation can be used; we foresters do not yet have the knowledge or the plant materials needed to copy this example in forest trees.

For some host-parasite combinations, trees have the disadvantage of a large size, limiting the usefulness of mixtures. The efficacy of the multiline in the small grains in resisting a leaf rust is partly based on the fact that each single host plant is long, narrow and relatively small. When a certain plant gets infected with a compatible race of the rust, a high proportion of the spores produced will be intercepted by the leaves of neighbouring plants which are not susceptible to this race. Conversely, from those neighbours, that plant will mostly receive rust spores of other races to which it is not susceptible. So a high proportion of the rust spores produced in the field will land on leaves where they cannot cause infections and thus will get lost. This mutual protection slows down the build-up of an epidemic; so the crop will be ripe before it can get severely rusted.

Such a reduction in the rate of multiplication of the parasite might be less pronounced in many tree diseases, simply because of the size of the host. In the large crown of a poplar, for example, a rust will find all neighbouring leaves equally susceptible and the build-up of the rust population will therefore scarcely be slowed down if the neighbouring poplar tree happens to be resistant to that rust. For many diseases, a single tree is large enough to allow a complete build-up of a population of the parasite; some diseases can take years for that process, as the tree does not move.

A useful delay in disease extension in a stand is not to be excluded for all host-parasite combinations and conditions. In a case where a disease spreads slowly from a focus, as may happen with a root rot that needs root contacts for its spread, it can be expected that a certain percentage of resistant trees (either of the same or of a different species) in the stand might effectively reduce the spread of the disease. If that same disease, however, can enter the same stand at many points, little will be left of such an effect of the resistant trees.

It follows that the extent of a possible retarding effect of a mixture of genotypes on the build-up of an epidemic will differ from case to case, and that only under very specific conditions a useful retarding effect may be anticipated. Thus the hope that mixing a more or less random collection of genotypes will improve the health of the individual trees seems mostly unwarranted.

It is sometimes suggested that genetic uniformity *per se* can increase the susceptibility of a stand to diseases. The above considerations make clear that this is hardly the case. Genetic diversity will rarely decrease the impact of a disease on the individual genotype, but it can decrease the risk by spreading it.

### Use of clones

Extensive planting of a single clone over large areas produces the extreme and horrifying situation of minimal genetic variation. Obviously, the use of clones can easily lead to reductions in the genetic variation, with all the negative effects and dangers mentioned. These are not inherent to all vegetative propagation, however. A wise production and use of clones can lead to genetic variation equal or even superior to that of seedling populations.

First of all it seems desirable to produce and release as many good clones as the nursery trade can reasonably handle, and keep more in stock and under test to substitute for those that need to be withdrawn. The clones should be of widely different genetic backgrounds. Here, vegetative propagation can make a big contribution to an increase of genetic variation in the planting stock. It allows the propagation of rare recombinants, hybrids and other outlying genotypes which cannot easily be maintained in seedling populations. Thus it is not difficult to maintain within a restricted number of clones a range of genetic diversity that is much wider than in a large seedling population.

The question remains, how clonal material should be used: in pure stands or in mixtures at the single tree level. Both seem acceptable un-

der certain conditions, both have specific pros and cons. Mixtures can utilize possible effects of GE-interaction, compensation and mutual protection and in some cases be more attractive for the eye. Unexpected damages can differ as to effects: slight damages, affecting a low percentage of the components will hardly be noticed in a mixture, especially if they occur in a young stage of the stand. They would however have a full impact on pure stands of that component. On the other hand, damage to a larger proportion of the components would leave all mixed stands defective; while if components were planted pure, some stands would be entirely undamaged whereas the others could be salvaged and replanted with better clones. Pure clonal stands may be easier on the silviculturist, the nursery-man, the designated authority for control of planting stock and on the industrial user; but if the clones are marketed pure and the balancing is left to the user, there is a danger that one or two clones will be favoured so that in the end they will constitute the majority of the plantings. In order to prevent this, each single released clone should have a high or specific usability. It can be advantageous to have both seedling populations and clones of a species on the market.

Mixtures are at a clear advantage in cases with many "unknowns" about the components, the sites, or their interactions. The same applies if the site varies considerably. If mixtures of many clones are desired — Kleinschmit (1977) prefers mixtures of over 100 clones — it may be better to release not the clones but the mixtures, and have their composition determined and guarded by a research station, a designated authority or some other organization with a long range responsibility.

From the foregoing it should be clear that genetic diversity in the planting stock provides no guarantee against diseases and damages. In many cases, however, it can limit their impact, first of all by spreading the risk, further by the mechanism of compensation, sometimes perhaps by reducing the rate of spread of a parasite.

For this and other reasons, genetic variation is an important goal for the breeder. It is his responsibility to maintain or develop genetic variation in his materials as he is supposed to be the person with the long range overview. If needed, he has to convince the nurseryman and the user of the wood of its advantage. Even though how much variation is needed cannot be defined, he should try to increase rather than decrease genetic variation.

A highly effective way to diversify is to use different species. This is so obvious that it should not be overlooked. Countries that depend heavily on one or two species should try to introduce additional suitable species. Countries that have a few major and many secondary species should resist the temptation to concentrate all their breeding efforts on the major species which would only accentuate their dominance. Instead, the secondary species should be improved too, so that a range of good propagating materials will be available to the planter. ■

FARMERS IN CENTRAL AMERICA MAINTAINING A TREE NURSERY
*combining forestry and agriculture*

References are at the back of the magazine, following the last article.

# Analysing benefits and costs of tree-breeding programmes

**A. Carlisle and A.H. Teich**

In recent times both scientists and natural resource managers have had to contend with the paradox that, although society realizes that science and products from natural resources are the life blood of civilization, there is an increasing reluctance on the part of governments to invest heavily in research or natural resource management, especially when this investment only pays off in the long term. Whatever the reasons for this situation, it is a fact that must be faced, and this, together with inflation, has resulted in keen competition for dwindling research and development money in all sectors. This in turn has resulted in an increased demand for programme justification, so that sometimes one seems to spend more time justifying research than doing the research. In this context of limited resources, it is vital that programmes are designed for maximum efficiency. If they can be made to pay off in the short term all the better.

Tree improvement programmes are very much a part of this picture. They can no longer be carried out as a matter of faith that tree improvement is the right thing to do and will probably pay off in the long run. This has to be demonstrated quantitatively, either by practical demonstration or predictive procedures. Most tree improvement programmes are handicapped by being long term and expensive, and may be looked upon with disfavour unless it can be shown that the probability that benefits will substantially exceed costs is very high. As Porterfield (1977) points out, because tree improvement is such a long term, expensive business, economic evaluation of the work is vital.

The purpose of this report is to discuss in general terms the contribution that economic analysis can make to tree improvement programmes. Other papers in this session by Reilly and Nikles (1977), Porterfield (1977) and van der Meiden (1977) deal with individual problems in greater depth.

Economic analysis has been used in tree improvement programmes in four ways:

- Programme justification — Does tree improvement pay?
- Programme optimization — What is the best tree improvement strategy in a particular situation?
- Selection of management alternatives — Should we invest in tree improvement, or silviculture, or mill process improvement, or all three?
- Identification of major cost sources in research and development programmes — Where does all the money go?

The problem with all these analyses, however, is that they are all in cash terms, and exclude many non-quantifiable benefits (e.g. crop security, product uniformity, aesthetics, etc.) that may be as important as the crop cash value, or more so. On the other hand costs can usually be computed precisely, so that we end up comparing minimal benefits with true costs. Fortunately most of the analyses carried out so far indicate strongly that tree improvement pays, in spite of this handicap, so there is no real problem in programme justification. However this imbalance is a potential source of error in programme optimization and selection of management alternatives, particularly the latter where the benefits of some alternatives are more easily quantified than others.

**Programme justification.** Tree improvement research and development can only be justified if they contribute appreciably to the success of operational tree planting and seeding programmes, or to improvement of trees

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used in urban situations for amenity purposes. A national relying wholly upon natural forests and natural regeneration for its forest products would not be able to justify a tree improvement programme. In contrast, such a programme is vital to a country relying wholly upon forest planting and seeding programmes to increase or maintain timber yield. Tree improvement has long been important to western Europe where natural forests have diminished considerably. However, even in a situation where planting and seeding programmes create a potential demand for improved tree seed, tree improvement — which aims at increasing crop security and yield, and producing the right kind of product — is only one of several management alternatives. It must be shown that it pays.

The majority of the reports in the literature of tree improvement economics are concerned with showing whether or not tree improvement programmes are profitable. Most of the authors use the method of discounted profits, comparing the expected profitability of the enterprises by comparing current values of future profits. For example, depending on the interest rate, a profit for which one has to wait ten years may only be worth half the amount now. The calculations use the compound interest equation. Also, most of the reports assume that it is necessary to allow for interest on tree improvement and tree establishment costs, adopting the attitude that one could just as well choose to invest in bonds as in tree improvement. This concept has met with some resistance from foresters who feel that this greatly inflates long term costs, and has resulted in a controversy, a red herring that has drawn attention away from the main fact that, even allowing for this cost weighting, tree improvement still seems to pay, provided the research and development results are ultimately used in forestry operations.

This report is not intended to be a comprehensive review of the literature dealing with tree improvement profitability, as this literature has been reviewed in other papers such as those by Carlisle and Teich (1971, 1975) and Dutrow (1974). However, in brief,

YEAR-OLD POPLAR CUTTINGS IN IRAQ
*making tree breeding pay*

although the potential of a tree to grow rapidly is controlled by several genes and is difficult to select and breed for, in most tree species we can expect at least 10% gain in growth, and in some 15% to 25% growth gains (e.g. Yeatman, 1974; Holst, 1971; Teich, 1973; Nikles, 1969). Trees can be selected for hardiness and, in some cases, resistance to insects or diseases such as *Cronartium fusiforme* or *Scleroderris lagerbergii* (Porterfield, 1964; Teich and Smerlis, 1969). Tree form and wood properties can also be selected and bred for.

All of these contribute to crop value and security or to efficiency of harvesting and manufacture of forest products. In the literature the evidence that these benefits considerably exceed the costs in cash terms is overwhelming. Davis (1967) found that for pines in the south eastern USA, even small increases in yield of 2.5% to 4.0% more than paid for the cost of improved seed, and other papers support this view (Perry and Wang, 1968; Bergman, 1968). We expect far greater gains from tree improvement programmes. Various rates of return on

investment in tree improvement programmes have been computed, ranging from 13.2% for poplar improvement programmes in the Netherlands and 12% to 20% in some of the USA southern pine programmes (e.g. Anon, 1975; Swofford, 1968; Porterfield, 1977) to the more modest 4.0% to 6.8% for red pine (*Pinus resinosa*) and jack pine (*P. banksiana*) in the USA (Lundgren and King, 1965) and 6.7% for white spruce (*Picea glauca*) in Canada (Carlisle and Teich, 1971). Davis (1969) showed that even a small (5%) increase in wood quality due to tree selection would raise mill profits by 15% to 41% by increasing yield of product per unit of wood processed and reducing mill processing time.

The report by van der Meiden (1977) describes the spectacular profitability of poplar (*Popolus*) breeding research in the Netherlands; the programme resulted in an increase in poplar wood output of 45% and an increase in cash output of over 50%. Also Reilly and Nikles (1977) clearly demonstrate the profitability of *Pinus caribaea* improvement in Australia.

None of the studies carried out so far indicate that tree improvement does not pay; it is usually just a question of which tree improvement strategy pays best. Again it must be emphasized that this favourable picture exists even though the benefits included in the calculations are minimal, excluding non-quantifiable benefits such as increasing crop security.

**Programme optimization.** In recent years the research on the economics of tree improvement programmes has shifted its emphasis from programme justification to programme optimization. The pioneers in this field are Van Buijtenen and Saitta (1972) and Porterfield (1974, 1975), all concerned with the southern pine programme of the United States. They used linear programming to "optimize the allocation of limited resources" available for tree improvement (Van Buijtenen and Saitta, 1972). The models assume a linear relationship between variables, absence of interactions between variables and constancy of the coefficients used. Van Buijtenen and Saitta (1972) used such a model to examine the consequences of roguing in seed orchards, and found that in their case (with southern pines) the maximum amount of roguing that could be done profitably was about 50%. They found that the use of a linear programming model forces the researcher to think systematically. More recently, Porterfield (1974) applied a multiple trait analysis to the southern USA loblolly pine (*Pinus taeda*) programme. A great deal is known about the genetics of this species and the economics of the operational programmes. A set of tree improvement goals were specified by the forest managers, and the mathematical model was used to find the best combination of tree traits to be selected and the optimum selection intensity for each trait. The traits used were bole volume, stem straightness, crown shape and size, wood specific gravity and resistance to fusiform rust (*Cronartium fusiforme*). The managers ranked these traits in order of importance, and decided upon a minimum desired percent gain. Porterfield used his model to optimize tree trait combinations and selection intensities so that the genetic improvement came close to programme goals. The economic return from the programme was also computed; using progeny testing and roguing the internal rates of return ranged from 10% to 14%, and without progeny testing, 8% to 13%. It was conservatively estimated that volume gains of 20% or more were possible by manipulating roguing intensity and wild stand selection expenditure. Reilly and Nikles (1977) report that in a *Pinus caribaea* var. *hondurensis* seed orchard in Australia, an internal rate of return of at least 14% was obtained without roguing, and a further 5% by effectively roguing.

Porterfield (1977) points out the a major part of on-going tree improvement programmes should be the examination of the effects of parameters upon profits, and consideration of the merit of selecting for each trait and the contribution of practices such as roguing.

Techniques of programme optimization are of great value in tree improvement programme planning and fund allocation. However, in order to use them efficiently, a great deal of basic genetic and economic information is needed, and this is sadly lacking in some tree improvement programmes.

In order to optimize returns from tree improvement research and development programmes it is necessary that the trees be capable of responding to selection and that the results from the programmes be extensively used. A small gain in growth or hardiness is of far greater value if the tree species concerned is planted or seeded over large areas than a much greater gain in a species planted on a limited range of sites. Before we can consider optimization of a tree improvement programme for a particular species, we must be sure that it is the right species, and that our eggs are in the right basket. Planning tree improvement programmes, therefore, requires a knowledge of species variability and an accurate prediction of the extent of future operational use, information that is not always readily available.

**Management alternatives.** Linear programming has a broader application than just the examination of alternative tree improvement strategies to optimize programmes; it can also be used to evaluate the effects of genetic selection and silviculture on wood and linerboard quality compared with the effects of technological control of linerboard quality during manufacture. It helps the manager to understand where to invest his money. An interesting study was carried out by T.L. Hart and A.E. Ferrie (1972) of MacMillan Bloedel Ltd.'s Operations Research Department in connection with the southern pine kraft linerboard programme. The aims were to "evaluate the extent to which quality of woody raw material can be modified by genetic and silvicultural means, in light of the investment required and the return expected", and to "compare the results obtained by this method of modification with the investment return picture of technological methods which will produce equivalent end-products". The example used was a hypothetical southern pine kraft linerboard mill producing 1 000 tons (907 metric tonnes) of 42 pound (19 kg) linerboard per day, 345 days per year. The

linerboard machine was fully integrated with a large scale pulp mill using batch digesters, and had an efficiency of 90%. Using the linear programming model to examine genetic, silvicultural and mill technology options, seven test cases were solved, using interest rates of 4% to 8%. The optimum solution for the forestry alternatives (genetic improvement, site preparation, fertilization) included, without exception, genetic improvement of such characteristics as volume production, specific gravity and disease resistance. On one soil type, a combination of genetic improvement and forest fertilization was the best option. Mill processing control of linerboard quality was emphasized more at the highest (8%) interest rate. The indicated return on the genetic improvement investment was 17%. It was found that in building the model and interpreting the results, many thought provoking questions were raised. The authors concluded that meaningful linear programming models can be constructed to examine forest management options and their effect on wood quality and volume and the interactions with mill processing. It is clear that models such as these are of great value in the decision-making process.

Again, this applies to a situation where there already exists a great deal of genetic information, economic data and processing techniques which can be incorporated into the model. For many species and situations this information is not available.

Even when subjected to this type of objective, rigorous scrutiny, tree improvement is shown not only to be economic, but to be the best of a number of options. By this time, surely, geneticists should be able to reduce their efforts of demonstrating to the policymakers that tree improvement pays, and move into the more rewarding field of programme optimization.

**Sources of costs.** Economic techniques, ranging from simple record keeping and accounting to complex mathematical models, can be used to identify major sources of cost. Tree improvement is a costly business and very often economic analyses tend to study costs and benefits from the seed orchard stage to the harvesting, often forgetting that before the seed orchard stage there may have been a large investment in research. However, in Canada an approximate calculation (Carlisle and Teich, 1971) indicated that, in the context of a 100 000 acre/year (40 469 ha/yr) white spruce planting programme, an expenditure of $1.5 million over a 15 year period on research, and $23 000 per year on seed production and collection, generates a potential economic benefit of about $832 000 per year on moderately fertile sites. So tree improvement still appears to be profitable when one includes basic research costs. Nevertheless it is vital that research costs are kept as low as possible without affecting efficiency. One of our studies (Carlisle and Teich, 1975), using unpublished data compiled by Paul Viidik of the Canadian Forestry Service, described the sources of costs in provenance trials and arboreta at Petawawa Experiment Station in Canada over a 50-year period. The total cost of the trials, in terms of present day wages, was about $2 500 per acre or $6 300 per hectare. By far the largest source of cost was in site clearance, at 325 man hours per acre (805 man hours per hectare) or, at present wage rates, about $1 950 per acre ($4 816 per hectare).

**Governments become increasingly reluctant to invest heavily in the kind of research that pays off only in the long term. This means that scientists can find themselves spending more time justifying research than doing it.**

Utilizing cut-over land for tree improvement experiments and seed orchards following harvesting operations, and thereby avoiding land clearance costs, is obviously much more economical.

Using a mathematical model, it has been shown that, allowing for interest and inflation, accumulated establishment costs far exceed management cost in a plantation operation at the time of harvest, indicating that establishment costs should be one of the prime targets for cost reduction (Carlisle and Teich, 1971). Tree improvement can help reduce these establishment costs by producing fast growing, hardy trees and minimizing tree losses and the need for costly tree replacement operations.

Estimating true costs is often hindered by the lack of adequate cost records. It would be of great value if detailed costs could be kept of all aspects of tree improvement.

In tree breeding programmes the selection of parent trees can involve considerable expenditure. Van Buijtenen and Saitta (1972) reported that 11% of total costs were attributable to this source, and Reilly and Nikles (*ibid*) found that for *Pinus caribaea* in Australia it was as high as 30% of the costs (when roguing costs were included) in a programme of selection and use of superior phenotypes for cloning and seed orchard establishment.

It is clear that economic techniques can play a useful role in tree improvement in programme justification, programme optimization, selection of management alternatives and major cost source identification. The most promising current trend is the increasing use of linear programming models to optimize tree improvement research and development; thereby increasing programme efficiency. However, these techniques require a great deal of genetic and economic input, and information in these areas is all too scarce in some programmes. The identification of these knowledge gaps and subsequent provision of the information should be of high priority in the future, so that limited research and development resources can be used most effectively. ■

References are at the back of the magazine, following the last article.

# Choosing strategies for the future

**G. Namkoong**

In our rapidly advancing field of forest genetics we have answered a lot of questions in recent years, but the answers have raised new and more difficult questions. We have learned enough techniques to be certain that we can develop new breeds. Now we need to look at what we have learned and decide how to organize breeding and gene management systems that will be the most beneficial to the future of mankind.

We have come to realize that the original gene pools are being physically lost. We have also begun to realize that unimproved gene pools will become economically useless as high yield breeds become incorporated into regular forestry practice. But with the power at hand to control the evolution of economically useful breeds, many questions need to be considered: in what directions should we develop future breeds? Should the nations or companies now bearing the cost of breeding programmes unilaterally direct the evolution of future tree breeds? How can we blend national and international objectives? How should we balance present with future obligations to people and forests?

The blending of national with international objectives is particularly difficult, and the complexity is increased by confusion about our exact obligations to future generations. It is clear that the design of a breeding system will be profoundly influenced by the inclusion of international objectives and future needs. It is not clear, however, how much weight the breeders of one nation should give to the needs of people in other places and times. According to Rawls' (1971) theory of justice, we should construct a system such that if a reasonable person is detached from any one particular place and time, he would judge that the costs and benefits of that system are fairly distributed. Then, the principle of equality dictates that we consider other people's needs as equal to our own and that we consider any time in the future to be as important as the present. If we accept something close to this idea, we must still ask who is going to pay the bills for other people and other times. Though all should bear some costs to reap some benefits, the poorest nations obviously cannot afford to match the richest nations in gene management. To support the principle of equality, the powerful nations and agencies will have to breed for other people's needs in addition to their own. And some method will have to be found to pay the bills. I believe that this can be done on utilitarian grounds.

A requirement that gene conservation and breeding efforts be efficient transcends geopolitical and time boundaries. We must also be constantly aware of technological and practical constraints as we consider long-term and often idealistic goals. In this report I will, therefore, first review our present technological status and gene management systems. I will, however, ignore some substantial current problems in production techniques and assume that sufficient seed or clonal propagates for reforestation can be produced from managed breeds.

### Present technology

The array of activities discussed in previous sessions is ample evidence of the importance, capacity, and economic feasibility of forest genetics technology. The purpose of this session is to discuss the ways in which our technology can be translated into breeding programmes under biological, economic, political, and personnel constraints. I am confident that improved breeds of trees can be produced under these constraints, but not without problems. I will first give some examples of excellent programmes that are under way.

The comprehensive Douglas-fir programme of the British Columbia Forest Service has all the ingredients of a complete, self-contained breeding system. Mr. Heaman (1977) has gathered both the data and the plant materials necessary for immediate gains and for future shifts as needs for change become apparent. The main materials are selected from the best available provenances and crossed in small, disconnected, blocked, partial diallel patterns which now include 350 parents. As they are found, additional materials are tested for inclusion.

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POLLINATING SPRUCE IN CANADA
*searching for the best combinations*

Samples from wider provenances are now being tested, along with inter-provenance hybrids. A large initial base population has been established and organized so that single or multiple breeds can be developed. The utility of breeding for specific combining abilities and for creating synthetic varieties with high specific or general combining ability will be determined, and the data and material for creating these breeds will be available. Since the tests are conducted on a range of sites, it will be possible to determine the value of breeding for specific sites and using genotype × environment interactions. Depending upon test results, the breeding population can either be combined or split into multiple breeds. Finally, seeds will be produced from orchards containing the best available subset of materials at a given time. The present materials in these orchards were selected for general adaptability, but future selection for orchards may well be on a different basis.

This programme emphasizes the maintenance of options for future breeding. Such heavy investment in the future implies a faith that reasonable genetic gains can continue to be achieved in successive generations of seed orchards. Critical factors in justifying the investment include forest ownership patterns and public attitudes toward forests in British Columbia. Almost all of the forest land there is owned by the Provincial Government, and the people are conscious of both their forest heritage and their economic dependence on forests.

The *Pinus radiata* programme in New Zealand evolved under somewhat similar constraints and therefore has similar objectives. Burdon, Shelbourne, and Wilcox (1977) examined a wide range of alternative mating designs for various purposes including estimates of variances and combining abilities, development of breeding populations, and production of seed.

They observe that no single design is best for all purposes and no single purpose need be served by only one design. The actual mating design used in each generation is also partly determined by the time and costs of obtaining various types of breeding material. In their programme, the

design used has changed from the first to the second generations. Their initial breeding material included about 600 seed parents. Their second generation material is obtained from their wind-pollinated offspring. For producing the third generation, crosses are currently being made in disconnected half diallels of five trees each.

Dr. Lindgren's (1977) work on mating designs suggests that reasonably good progeny tests can be made with a limited number of trees in any of several designs including common testers, partial diallels, poly crossers, and open pollinations in seed orchards. Designs therefore can be chosen primarily for their usefulness in breed production or variance estimating.

In developing a broad breeding programme for *Eucalyptus* in Papua New Guinea, John Davidson (1977) was faced with different constraints. As a result, the breeding programme there is quite different. Short timber rotations and the achievement of sexual maturity at a low age for *Eucalyptus* permit full breeding generations to be cycled in five years. A large array of studies on genetic variation and breeding techniques therefore have already been completed in natural stands and in provenance and other plantings. Heritabilities for growth and wood quality traits have been estimated; and populations, families, and individuals promising substantial gain have already been selected and tested. Cutting and grafted seed orchards and seedling seed orchards are all being used, and their relative efficiencies are being compared.

Current seed production comes from 28-50 parents, but a new breeding programme involving 150 parents is being developed. It will include family and individual selection and single pair matings. In addition, provenance collections and other assorted materials will serve as a gene reservoir. Thus, in this fast-developing programme the value of improved varieties has already been demonstrated, provision has been made to satisfy immediate needs for improved seeds, and a population has been provided for future evolution.

The financing of this programme is largely external. Supporters of the programme may view some of the benefits as altruistic or political and some as indirect. The indirect benefits of establishing this programme would include gaining of information and experience that might prove useful in other programmes or with other species elsewhere. The programme may also be viewed as an attempt by one community to improve the well-being of a more inclusive community with other people and times.

The benefits of international cooperation in breeding programmes are sometimes both immediate and direct. Burley and Nikles (1977) describe the organization of an international breeding programme for tropical pines. A network of breeding populations has been established in which increases in yield are being obtained at various locations. The size of the genotype × environment interaction is the key factor in determining whether to develop special locally adapted breeds or more generally adapted ones.

**Success in any breeding programme depends largely upon having the right data when you need it. Data problems exist . . . and they are more than a minor hindrance.**

There is ample evidence that immediate gains can be achieved with only preliminary data and simple breeding techniques from breeding populations of various sizes. We also know that, by increasing population size and complexity, provision can be made for future uses. With some further increase in complexity, a programme can also become international in scope. Since various forms of international cooperation already exist, it seems clear that there are advantages to this approach.

Success in any breeding programme depends largely upon having the right data when you need it. As the complexity of the programme increases, so does the complexity of the data collection, handling, and storage. Data problems exist, and they are more than a minor hindrance.

Data recording and storage for future use can be a weak link in the breeding process, particularly when information is needed about juvenile-mature correlations. While the inevitable missing data and irregular format problems can be handled by subroutines, the necessary analyses may be too difficult for the typical tree breeder. Furthermore, since forestry experiments are costly and time consuming, all forestry data are expensive. Hence, we must make best use of the data we have through analytical procedures of maximal efficiency. New research on estimation procedures such as quadratic estimators would be important for forestry experiments.

In multiple-trait selection, data problems are especially critical. Franklin and Stonecypher (1977) show that use of variances and covariances in index selection is important for maximizing gain. But they also show that estimation errors are often damagingly high. One dilemma is that trait correlations which affect gain cannot be ignored but that these correlations can only be approximated with uncertain error.

Despite these difficulties, Burdon, Shelbourne, and Wilcox (1977) feel that in *Pinus radiata*, long term pedigreed breeding populations promise enough genetic gains to warrant the effort involved. Selection at young ages is also considered to be a worthwhile attempt for accelerating the genetic gain rate. They propose a hierarchy of populations — one for seed production, a larger one for breeding, and a still larger one as a gene pool. Advances in the breeding population are achieved through recurrent selection, and nonrecurring bonus gains are obtained by secondary selection in the seed production population. This programme is similar to that proposed by Namkoong *et al.*. (1971) with the addition of an unimproved gene pool population. They also suggest that the breeding population be

split into sublines which may undergo inbreeding but can be intercrossed for seed production. This proposal is similar to that of Baker and Curnow (1969), except that the latter authors recommend selective elimination of some sublines.

### Managing genetic resources

If it is clear that we can change breeding populations and their derived seed populations in ways that appear useful, it is also clear that to achieve these gains requires important choices. The breeder must compare costs with benefits and, perhaps more importantly, he must limit population size. In a sense, when a breeder decides not to improve a particular species he chooses a gene pool, a population size, and a set of selection coefficients — he accepts the values that accidentally occur in nature. When he decides to breed, he must choose a reduced size for the population and gene pool; these reductions are achieved by selecting for some specific combination of traits. He might allow the desire for immediate gains to cause him to reduce the gene pool so much that the remainder is undesirable in some way. Intensive selection in a single population down to less than eight parents maximizes the selection differential and expected gain for this generation at a large expense in genetic variations for gains in future generations. Less intensive selection, with larger population sizes, reduces present gains in seed populations but leaves more opportunities for future gains. The breeder can make such choices less painful through careful selection of breeding designs, but difficult choices will always remain.

The hierarchial breeding system recommended by Burdon, Shelbourne, and Wilcox (1977) is an attractive way to resolve the conflict between present and future gains. In this system the gain achieved in the seed population does not affect the long-term gain potential of the breeding population, which is less intensively selected. Furthermore, advances in the breeding population are backed up by a reservoir in an unselected gene pool population. If the system has a weakness it is the present and continuing cost of maintaining this unimproved gene pool population which may never be used and can be used only with great difficulty. The system's large breeding population implies relatively slow present gains. It is felt that the reductions in present gains will be offset by increases in future gains. Such a choice seems justified in many cases.

An alternative system of breeding multiple populations may also prove feasible. Dividing the breeding population into subunits can achieve more gain than selection with comparable numbers in a single breeding population (Baker and Curnow, 1969). When the future is uncertain, selecting in several subunits for different trait combinations or site conditions can give greater expected gain than single-population selection (Namkoong, 1976). Deployment of multiple populations in several directions around combinations of high expected value can give high immediate gains, guard against selection in an improper direction, and provide for future population flexibility and variation. This strategy is similar to those adopted by experimental designers who seek to place sample points near critical or extreme points. Samples are deployed to assure that the critical points are well encircled. In designing the future evolution of forest tree species, we should consider such multiple deployment of small breeding subpopulations.

**We and our inheritors all inhabit one planet with a common array of species to develop. The need for joint programmes on gene-pool evolution is obvious.**

If we must strike a balance between present and future gains, we must also strike one between national and international objectives. Nations bear unequal burdens and reap unequal benefits, and regardless of national aspirations, present and future generations may unequally share the costs and profits. Selection for a forest management system profitable to one agency may not be best for another. Just as we must accept reduced immediate progress to ensure future gains, we must make some sacrifices to accommodate conflicting aims. Hierarchical breeding systems have the simplest organization for such accommodations, but multiple breeding subunits are also a possibility. The multiple approach promises more security of gains but is harder to manage. The optimal system will undoubtedly vary by species or species group.

Since we and our inheritors all inhabit one planet with a common array of species to develop for greater or lesser use, the need for joint breed management programmes seems obvious. If we can afford joint programmes on gene pool conservation, we can surely afford joint programmes on gene pool evolution to manage them for diverse goals. The work of the Commonwealth Forestry Institute and the many bilateral efforts in breed development should be continued and supported. To assure international cooperation in complex gene management systems, FAO and IUFRO might assume at least planning responsibility. In such systems, intercrossing and overall population deployment could be managed internationally, and individual nations and agencies could develop special programmes to satisfy immediate needs from the hierarchical sub-breeds or from semi-independent multiple breeds. Short-term breeding goals could then be accommodated in long-term programmes with international objectives. The experience of IUFRO in cooperative work on species breeding and gene conservation might be extended to a more general programme under FAO auspices. ■

References are at the back of the magazine, following the last article.

# Reproductive habits of the eucalypts

L.D. Pryor

The last decade has seen tremendous expansion in the use of Eucalyptus in plantation silviculture in the warm, temperate and monsoon tropical regions of the world. The capacity of species of the genus to produce wood quickly on short rotations, in a form suited for both industrial and rural use and in climates frequently rather severe in terms of moisture relations for tree growth, has contributed to its success in many countries in the warmer latitudes of the world. Much of this good performance is due to the absence of leaf-eating insects which are so much a feature of the natural eucalypt habitat. But it is also due to silvicultural methods which have become routine practice in plantation silviculture with the genus, especially methods of soil cultivation and fertilizing. Large and still growing demands for pulp, paper and other wood fibre products have led to some very large plantation schemes. The capacity of the eucalypt to endure rather harsh conditions and yet make stems of reasonable form and dimensions, has made it of particular importance in the rural economies of many developing countries.

It has recently been reported that there is now more Eucalyptus wood utilized outside Australia than within and this situation will become accentuated as time goes by.

Eucalypts are confined naturally to the Australasian region where there are some 450 quite distinct species and numerous variants within many of them, so that it is a formidable task to screen the genus to select a species likely to be the most suitable for a particular locality. The sheer weight of species numbers alone has presented problems of organization which often strain local resources of countries other than Australia carrying out silvicultural programmes. The preservation of the natural gene resource in Australasia for future world silvicultural development is certainly one of the pressing needs in Eucalyptus improvement. The benefits will be especially felt in the future rather than the present.

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## Natural habitat

Eucalyptus in its many species provides the arboreal vegetation (mainly forest and woodland) of more than half Australia. It occurs to a very limited extent in Papua New Guinea, Mindanao, Celebes and Timor and some of the Lesser Sunda Islands of Indonesia. Like many woody genera, Eucalyptus is predominantly a randomly outbreeding genus depending very largely on insect vectors for pollination and — with one or two exceptions — without any significant vegetative multiplication taking part in reproduction under natural conditions. The numerous species which occur throughout the natural range of the genus make it unusual, if not unique amongst woody plants, especially for the great sensitivity of numerous species to habitat and the fact that individual stands of a species are often of limited extent. Those species which are extensively distributed generally show considerable intraspecific variation.

A starting point in the improvement of Eucalyptus is with the systematics of the genus, an area of research which is complex for a plant group and the object of continuous study. Undoubtedly, most species of eucalypts are well known and a good deal of current study is simply a systematic reinterpretation of already known material. But increased activity in botanical exploration within Australia, especially of sites often of limited extent and opened up relatively recently to easy access, has disclosed additional species not previously known and it must be expected that still more will be recognized and described in the future, although as little as 20 years ago it seemed there would be few still to be recognized. It is quite unlikely that any species with an extensive distribution and in large stands remains to be discovered although some redefinition of species represented by extensive populations may still be expected. Systematic studies therefore remain a significant element in improvement work and will have substantial impact in future developments in the silvicultural improvement of the genus.

Virtually without exception the species regenerate by seed with supplementary survival through vigorous vegetative rejuvenation of damaged individuals whether this be by fire, drought, grazing or man.

It is indicated from so far relatively limited studies that species are generally preferentially outcrossed but some at least include a proportion of selfing although this may be associated with a loss of vigour in selfed offspring.

Self incompatibility occurs in varying degrees; it is known in a number of species and clearly has a bearing on

PLANTATION OF *Eucalyptus deglupta* IN PAPUA NEW GUINEA
*breeding for tropical conditions*

their reproductive habits. In the natural stands, providing there is no substantial habitat disturbance, the species for the most part are evidently quite stable and genetic breakdown between them does not readily occur. There are exceptions in some localities but, overwhelmingly, the majority of species retain their identity unblemished even though some limited interspecific hybridizing may, and often does, take place between pairs of species when they are growing side by side and are cross compatible. If there is no human disturbance the products of this hybridizing seldom have been able to spread from the site of initiation to others. The breeding system implies a high level of genetic diversity in each species. This is, on the one hand, often a disability for immediate silvicultural use but, on the other, it ensures an array of genotypes which is one of the bases for tree improvement work. It implies that there is an opportunity for very great improvement by well known means. For many species, generation time is often six or seven years from seedling to the production of the first seed crop, although there are a good many exceptions in which flowering may take place as early as the second year and, occasionally, one-year-old plants are known to produce flower buds and set seed. In tree improvement work this is quite rapid and there are benefits to be had from this relatively short time scale. Seed for most species takes from six to twelve months to ripen which is a further cause for delay. This, together with long gen-

eration time makes any breeding programme dependent upon a sequence of generations a rather slow and tedious process. As a consequence, the principal thrust for improvement work in the next few decades will be by means of those techniques which do not depend on a turnover of generations. On the other hand, the seed is quite small and a kilogramme from most species will produce a very large number of seedlings, five hundred thousand being common enough.

### Variation

Because of the very substantial genetic variation in species, it must be assumed that the process of natural selection which has been going on for a very long time in the Australian habitat has led in many cases to very precise site adaptation so that separate populations within species of Eucalyptus generally differ one from the other throughout the geographic and climatic range of the species. This capacity for precise site adaptation is quite general in eucalypts and is a condition of basic value in any improvement programme. The amplitude of this variation is readily assessed only for the climatic and edaphic range of the natural habitat. Because of Australian topographic and edaphic characteristics and latitudinal location it does not offer always the opportunity for selection for particular climatic conditions by a homoclime comparison. This is especially so with regard to the ability to endure low temperatures and — in a lesser way — to adaptation to calcareous soils. Many species are able to thrive as a silvicultural crop in site conditions distinctly different from those of any part of their natural habitat. Evidence of such capacity depends on the known results of trials with any given species planted as exotic and therefore accurate records of performance of eucalypt species planted outside Australasia are vital to the assessment of the potential ecological amplitude of each; a good example is seen in *E. camaldulensis* which has been very successful in northern latitudes of more than 42°, whereas it is limited to about 38° in Australia and *E. globulus* thrives in low latitudes and high altitudes in India (Octacamunde) and also on the Alto Plano of Bolivia although it does not occur naturally above 500 m altitude or below 36° of latitude.

The designation of species depends upon systematic treatment. In plant groups this is not uniform, partly because different authors have had somewhat different standards, but also because, in some taxa, groups that may reasonably be recognized as species are not always the same in their characteristics from genus to genus. Broadly, eucalypt species occur in two ways in relation to their total populations. Firstly, there are those species of limited geographic extent and unusual habitats represented by small populations confined to particular sites either of climatic or edaphic conditions. The size of the natural populations is not necessarily an index to the utility of the species in silviculture. Some successful or potentially very successful ones have come naturally from extremely limited sites indeed, as for example *E. dunnii*. On the other hand, there are species with quite extensive geographic ranges covering distances of hundreds, even thousands of kilometres and in altitude hundreds of metres, within which there is considerable population diversity. This is usually reflected through different genetic make up in the different stands. There are of course intermediate circumstances. One of the general features in species of Eucalyptus which are widespread, apart from variation in accordance with different sites, is the graded variation which is associated with graded habit conditions. This is clinal variation, which is usually recognized on the basis of morphology but appears to be almost always accompanied by gradation in physiological features too. Clinal variation presents problems in terms of systematics but provides a genetic condition of high value in terms of tree improvement. Some of the most important species display variation of this type throughout their range and therefore a knowledge of such patterns is of weighty significance when searching for the best provenance for any particular silvicultural use.

The first step in any tree improvement programme is the designation of species and their introduction for trial. A principal shortcoming or source of error, often is the precise identity of the material involved, since it is easy and at several points possible to have misidentifications which can be quite misleading. However, once a species is known as likely to be successful — if it is one which is at all widespread in its natural stands — then a very considerable genetic diversity can be expected in the natural populations, and precise attention to provenance of seed together with trial plots to determine which provenance is most suited to the project becomes essential. Many of the physiological characters which depend upon provenance are those related to climate, a capacity to withstand lower than usual temperature being one of the so far most examined. There are also species, provenances of which may occur on special sites such as calcareous soils, where in most of the range the species is on non-calcareous substrata. This may provide an opportunity for the introduction of provenances with the physiological capacity to endure calcareous sites which the species for the most part cannot tolerate well, as for example, in *E. camaldulensis*. The same applies to ability to resist saline conditions and to other special physiological capacities.

### Interspecific hybrids

The formation of viable hybrids between pairs of species is common enough in many plant genera. On the other hand, in some groups of plants this is absent. In eucalypts the occurrence of interspecific hybrids is common but species breakdown seems to have been avoided in the natural circumstances largely by an economical barrier. Interspecific hybrids occur at stand junctions but their progeny is limited and they do not invade the parent stands. If this isolating situation is circumvented or eliminated, either by human interference with the natural habitat as has occurred very extensively in Australia in the last two hundred years, or the elimination of it when the species are

planted together as exotics, interspecific hybridizing may become extensive. There are recognized in Eucalyptus some seven or eight taxa which might be ranked as subgenera and between which it appears that hybridizing does not occur but within which it is usually found from rarely to frequently between some pairs of species. It is relatively easy to find individual trees in the field which are hybrid between many pairs of species, capable of interbreeding when they occur naturally side by side. It is less usual in the natural habitat to find extensive breakdown between species except perhaps in excessively disturbed areas where conditions have favoured the spread of consequent hybrid swarms. Because of the size of the genus and the features by which the species are recognized and classified it is not always easy to recognize naturally occurring interspecific hybrids. To be reasonably sure that any suspect individual is a hybrid, rather rigorous examination is necessary by proceeding beyond morphological and field examination to look at least at the progeny from an open pollinated seed set. In spite of the fact that interspecific hybridizing is generally not associated with a genetic breakdown between species there are a few circumstances where in the natural environment there has been interspecific mixing on a fairly extensive scale and areas where such genetic intergrades occur. This poses both particular problems and opportunities for tree improvement. Such breakdowns in the natural stands evidently depend on unusual natural conditioning circumstances.

The position with regard to interspecific hybrids is of special importance for an introduction programme. There is no doubt that in the past seed has left Australia already interspecifically hybridized because in seed collection this condition has been overlooked (for example *E.* "*algeriensis*" and *E. rudis*). At times also interspecific hybrids have occurred in exotic collections from which seed has been produced and has further complicated the matter of species choice. This is not only because in subsequent generations after initial trials there is genetic degrade of the material, but also because the $F_1$ interspecific crosses in a number of cases give stands of superior value. The bringing together in arboreta of collections of species not ordinarily associated in the natural environment is a potent source of interspecific hybridizing and one which has had a major impact in the situation in some countries. Where this has occurred successive generations of Eucalyptus derived from an initial hybrid source show a pattern of segregation which leads to very considerable degrade in the quality of subsequently produced stands as a whole as for example in Brazil with *E. urophylla*.

This situation leads to a condition in which to arrest declining productivity there must be a return to pure species and a programme to ensure the elimination of such genetic contamination.

## Improvements

There is a long way to go and tremendous opportunities in this field. Some of the ultimate potential is dependent on technical developments which will have an impact on tree species improvement generally. These are techniques such as clonal culture either by meristem or single cell culture or by some method of raising trees not at present susceptible to the method, by stem cuttings. A breakthrough in any of these methods to permit clonal culture will open the way to considerable improvement, with at the same time the introduction of risks and pitfalls against which adequate safeguards should be built into any programmes so implemented. Until such radical developments occur some of the steps which can be taken have been explored in eucalypts so that programmes which apply to them can be taken up with confidence where there is a substantial silvicultural operation foreshadowed or in existence.

## Seed production

The first step in eucalypt improvement is to obtain in a particular area the provenance of a species most suited for the purpose. Once a species has been designated as that desired, then if there is variation from natural provenances in performance it should be examined fully. In most eucalypt species there is such variation and a programme to enable designation of the best source can lead to very substantial gains. In a great many cases — probably in most cases — seed in the quantities needed for a significant programme must be produced in cultivated stands since supply from the natural provenances is now generally limited. This, however, will become increasingly so as time goes on, not only because there are variations from year to year in the seed crop, but the natural stands are diminishing rather than increasing and are more and more being placed under long term protection so that procurement can be ensured in continuity for experimental plots but is unlikely to be maintained in lots suitable for large scale commercial activity.

Thus the development of seed producing plantations becomes particularly important. This can follow two general patterns: firstly, seedling seed orchards or seed producing plantations which do no more than maintain the genetic integrity of the species and the particular provenance involved by ensuring that it is suitably isolated from potentially contaminating genetic sources. The maximum distance from another stand with which a given stand can easily cross is dependent for the most part upon the distance that insect vectors travel to effect pollination. It appears that two kilometres is ample distance in most cases but the number of assessments of this is still small and attention should be given to accumulating information on this aspect. A very effective way of isolating seed producing areas is to plant the seed producing plot in a plantation of another species with which there is a complete barrier to interbreeding. Because more than one species often is used in silvicultural programmes this is quite often feasible. For example, isolation can be provided by *E. citriodora* if the seed producing plot is to be *E. grandis* or *E. saligna*, and for given species such arrangements can be planned. The seed producing plots themselves should be planted at reasonably close spacing to allow early and heavy thinning so that trees of the best form and vigour are retained for culling at rather wide

spacings so that full crowns will develop and good seed crops result. Enough experience has been gained to show that systems of this kind work well although the precise details of spacing, time of thinning, methods of seed collection from often finally large trees have to be worked out in accordance with the facilities in the locality in which the programme is implemented.

### Clonal seed orchards

A further step is in the development of clonal seed orchards where the theoretical background which has been used, particularly with regard to Pinus, appears to have full relevance in Eucalyptus although evaluation of the genetic gain in eucalyptus still awaits precise assessment for such orchards. As with pine, it has been found that grafted clones tend to display a rather high proportion of graft incompatibility which can be circumvented only by having many replacements so that there will be enough compatible grafts to make up ultimately the clonal population in the orchard. Unfortunately, as with pines, it is not always possible to foresee in young grafted stock even up to a year or two old which will be compatible and there are good reasons for avoiding this problem where possible. In some species of economic importance it is known this can be done effectively by growing clones from cuttings even though there are considerable constraints at present in the way cuttings may be taken. This varies from *E. deglupta* in which striking from cuttings is easy even from quite old material so that a clonal seed orchard can be built up this way or even by using air layers from quite large trees, which is also very successful. There are indications that some other species may be fairly easily handled this way too but the large majority of eucalypts will not strike from cuttings or form roots on air layers once the plant has proceeded significantly beyond the juvenile stage. With fast growing species such as *E. grandis*, selections can be made from trees already of substantial stature at four or five years of age by felling outer lines in plantations and selecting the best trees in these lines. Coppice shoots from the stump will strike quite readily from most trees giving at least 50% average success, provided they are taken under Australian conditions during three or four months of spring or early summer. Then they strike readily under standard mist spray. Research and development has proceeded sufficiently far to indicate that this is a highly successful method and the development of seed orchards on this basis has been accomplished in *E. grandis* and *E. saligna*. It may be found when fully examined to apply to many other eucalypt species. The possibility of rejuvenation of cutting material by subculturing from some initially established cuttings, even where the first established ones may have been difficult to strike, is a developmental aspect which merits thorough exploration. This is evidently a phenomenon exploited traditionally in horticultural plants and it appears the same occurs in at least one species of eucalypt, *E. Camaldulensis*.

Il seems possible that even if the initial clonal development depends on grafting, rejuvenation of the scion may follow with progressive subculturing by cuttings.

### $F_1$ manipulated hybrids

There is strong evidence to show that interspecific $F_1$ hybrids frequently will outperform pure species in terms of desirable produce. The production of interspecific $F_1$ hybrids spontaneously and unintentionally, and especially the incorporation of their offspring in plantations, can be a source of degrade as outlined earlier. On the other hand, if this could be exploited in the way that the use of hybrids has been in some agricultural crops, there is no doubt that a very considerable improvement in production would follow.

One of the most effective systems can be found in an advanced experimental stage in Zambia. It involves production of hybrids between *E. tereticornis* and *E. grandis* simply by planting the species together in seed producing areas and roguing the progeny to select the $F_1$ hybrids. This can be done visually with ease. While this is a programme that has a degree of chance and unpredictability as to the quantities produced, it does work but it hinges upon a peculiarity which is almost confined to *E. tereticornis* in that this species is in part at least wind pollinated and there is no need for particular manipulation to secure seed set which occurs in part at least when *E. grandis* is planted nearby. Various refinements to this system are possible such as the clonal production of *E. grandis* individuals known to be fully self incompatible. These are known to exist. In addition, manipulated pollination to increase seed set may be appropriate even in this wind pollinated species. With the large majority of eucalypts, however, it is necessary to carry out fully manipulated crossings and there are certain parts of this operation which have not yet been developed to a production scale. If self incompatible clones of the female parent are built up — and these could be done by grafting where graft incompatibility is of less significance than otherwise — emasculation will not be necessary and stored pollen can then be placed by hand on the stigma of the female parent to be followed by seed set. The evidence from spontaneously occurring hybrids such as the well known *E.X. trabutii* (an interspecific hybrid between *E. botryoides* and *E. camaldulensis*) which has performed so very well in the Mediterranean area, or the numerous cases where hybrids between *E. tereticornis* and *E. saligna* or *E. tereticornis* and *E. grandis* have been seen to perform well, together with more precise experimental trials of other interspecific hybrid combinations, indicate that this is a method of very considerable potential.

It has been shown in many combinations that $F_1$ interspecific hybrids have a high level of uniformity — at times more so than that of the parent populations themselves.

The use of interspecific hybrids opens the way for the production of combinations which will sometimes bring together the most economically desirable characters from a pair of species. At present, the nature of the $F_1$ in this way and therefore its economic value is not readily predicted and evaluation depends on actual trials. ■

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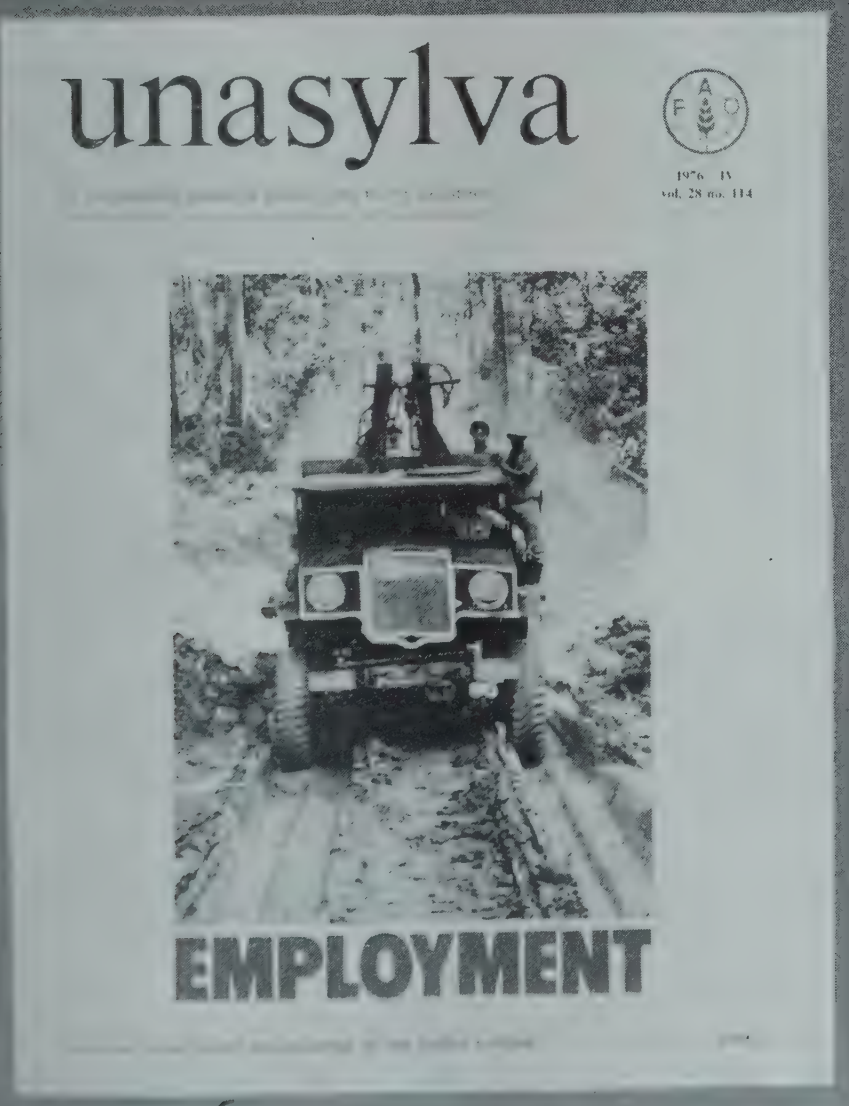


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# Consultation documents

These are the papers which were presented at the consultation. They are published in the Proceedings of the consultation in the languages indicated by the titles in this list. It can be seen that the principal papers have been translated and appear in English, French and Spanish, while the others are published only in the language in which they were written.

A copy of the Proceedings may be obtained by writing to CSIRO, Division of Forestry Research, Canberra, A.C.T., Australia.

### Keynote address

BRUCE J. ZOBEL, E.F. Conger Distinguished Professor

The good life or subsistence — how tree breeding can help (FO-FTB-77-0/1)

*Bien vivre ou subsister — contribution de la génétique forestière*

*Una vida mejor o la mera subsistencia — la ayuda que proporciona el cultivo de los árboles*

### Invited lecture

L.D. PRYOR, Emeritus Professor, Australian National University

Breeding habits of the eucalypts in relation to introduction and improvements throughout the world (FO-FTB-77-0/2)

*Modes de reproduction de l'*Eucalyptus *considérés sous l'angle de l'introduction et de l'amélioration dans le monde*

*Los hábitos reproductivos del* Eucalyptus *en relación con su introducción y mejora en todo el mundo*

### Position papers

R.H. KEMP

Exploration, utilization and conservation of gene resources (FO-FTB-77-1/1)

*Prospection, exploitation et conservation des resources génétiques*

*Prospección, utilización y conservación de recursos de genes*

J.F. LACAZE

Progrès dans le domaine de la sélection d'espèces et de provenances (FO-FTB-77-2/1)

*Advances in species and provenance selection*

*Progreso alcanzado en la selección de especies y de procedencias*

D.P. FOWLER

Population improvement and hybridization (FO-FTB-77-3/1)

*Amélioration des populations et hybridation*

*Mejora e hibridación de poblaciones*

H.M. HEYBROEK

Multiplication and genetic diversity as factors in the employment of genetically improved materials (FO-FTB-77-4/1)

*Importance de la multiplication et de la diversité génétique dans l'utilisation de matériel génétique amélioré*

*La multiplicación y la diversidad genética como factores del empleo de materiales genéticamente mejorados*

A.H. TEICH AND A. CARLISLE

Analysing benefits and costs of tree breeding programmes (FO-FTB-77-5/1)

*Analyse du coût et des avantages des programmes d'amélioration des essences forestières*

*Análisis de costos y beneficios en programas de mejora genética forestal*

G. NAMKOONG

Choosing strategies for the future (FO-FTB-77-6/1)

*Le choix de stratégies pour l'avenir*

*Elección de estrategias para el futuro*

### Invited special papers and voluntary papers

O.H. FRANKEL

Philosophy and strategy of genetic conservation in plants (FO-FTB-77-1/2)

H. KEIDING AND R.H. KEMP

Exploration, collection and investigation of gene resources: tropical pines and teak (FO-FTB-77-1/3)

J.W. TURNBULL

Exploration and conservation of eucalypt gene resources (FO-FTB-77-1/4)

R. KOSTER

Conservation and study of genetic resources of poplars (FO-FTB-77-1/5)

R.E. SCHOENIKE

Assessment of gene resources in *Cupressus arizonica* in the United States (FO-FTB-77-1/6)

J. DAVIDSON

Exploration, collection, conservation and utilization of the gene resources of tropical *Eucalyptus deglupta* (FO-FTB-77-1/7)

J. SAMEJIMA

Genetically controlled forest in Hokkaido, Japan (FO-FTB-77-1/8)

V. ENESCU, L. CONTESCU and A. GRIGORESCU

On the preservation and utilization of the genetic forest resources in Romania (FO-FTB-77-1/9)

J. DIETRICHSON AND R. LINES

Recent advances from international cooperation in species and provenance selection within the temperate region (FO-FTB-77-2/2)

P.J. WOOD and A. GREAVES

Advances from international cooperation in tropical pines (FO-FTB-77-2/3)

S.P.K. BRITWUM

Species and provenance selection of tropical hardwood species with special reference to West Africa (FO-FTB-77-2/4)

B. MARTIN

L'*Eucalyptus* comme exotique: récents progrès dans le choix des espèces et des provenances (FO-FTB-77-2/5)

F. OWINO

Selection of species and provenances for afforestation in East Africa (FO-FTB-77-2/6)

J.T.A. GURGEL and G.R.A. CAVALCANTI

Behaviour and survival of *Eucalyptus* sp. in the state of São Paulo, Brazil (FO-FTB-77-2/7)

M.A.K. KHALIL

Role of exotic species and provenances in forest improvement in Newfoundland (FO-FTB-77-2/8)

R.K. ORME

*Eucalyptus globulus* provenances (FO-FTB-77-2/9)

C. Palmberg

Selecting for rust resistance in poplars in Australia (FO-FTB-77-2/10)

J. Piot

Essai de 10 provenances de teck en Haute Volta (FO-FTB-77-2/11)

J. Piot

Essais de provenances d'*Eucalyptus camaldulensis* en Haute Volta (FO-FTB-77-2/12)

A.E. Squillace, D.G. Nikles and L.C. Saylor

Monoterpene composition in cortical oleoresin of *Pinus caribaea* and relation to *P. elliottii* of Florida (FO-FTB-77-2/13)

J. Delaunay

Résultats d'un essai international de provenances de Cedrela, sept ans et demi après sa mise en place en Côte-d'Ivoire (FO-FTB-77-2/14)

J. Delaunay

Résultats d'essais de provenances de teck, *Tectona grandis*, deux ans après leur mise en place en Côte-d'Ivoire (FO-FTB-77-2/15)

J. Delaunay

Résultats d'essais de provenances de teck, *Tectona grandis*, six ans après leur mise en place en Côte-d'Ivoire (FO-FTB-77-2/16)

J. Delaunay

Premiers résultats des essais de provenances de *Terminalia ivorensis*, deux ans et demi après leur mise en place en Côte d'Ivoire (FO-FTB-77-2/17)

J. Delaunay

Les essais de provenances de *Terminalia superba*, six ans après leur mise en place en Côte-d'Ivoire (FO-FTB-77-2/18)

K. Diabate

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K. Diabate

Premiers résultats des essais de provenances de *Pinus caribaea* Morelet mis en place en 1971 et 1972 à San Pedro (Côte-d'Ivoire) (FO-FTB-77-2/20)

K. Diabate

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F. Grison

Variabilité génétique de l'Okoumé. Essais de provenances et de descendances (FO-FTB-77-2/22)

R.W. Fishwick

Results of provenance trials of *Pinus* species in southern Brazil (FO-FTB-77-2/23)

C. Barbier

Introduction et sélection des *Eucalyptus* au Niger (FO-FTB-77-2/24)

F. Wencelius

Plantation comparative de provenances de *Pinus caribaea* (FO-FTB-77-2/25)

J. Davidson

Advances from international cooperation on tropical *Eucalyptus* (FO-FTB-77-2/26)

Y.P. de Castro Pasztor

A provenance trial with *Eucalyptus pilularis* Sm. (FO-FTB-77-2/27)

Y.P. de Castro Pasztor and L.C. Costa Coelho

A provenance trial with *Eucalyptus maculata* Hook: preliminary results (FO-FTB-77-2/28)

J.F. Lacaze

Etude de l'adaptation écologique des *Eucalyptus*; étude de provenances d'*Eucalyptus camaldulensis*. Project FAO No. 6 (FO-FTB-77-2/29)

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A. Grigorescu

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A. Grigorescu

On the growths of some black pine provenances in a nursery test (FO-FTB-77-2/33)

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**Recommendations from**

# the third World Consultation on Forest Tree Breeding

Three World Consultations on Forest Tree Breeding have now been held: the first focused on the principles of forest genetics; the second emphasized the benefits which accrue from tree breeding and the mass production and utilization of improved seed; while the theme of this third consultation was "strategies in forest tree breeding with special reference to the tropics."

During the eight years since the last consultation there has been an increasing awareness that the identification and breeding of superior genotypes must be complemented by measures to reduce gene loss and conserve genetic diversity. As genes and genotypes of little immediate commercial importance may become valuable in the future, the conservation of genetic resources should be considered of paramount importance for tree breeding programmes. Maintaining genetic diversity, either within a species being improved, or by using several species for afforestation programmes, also serves as insurance against unknown risks and may facilitate the breeding of special genotypes for particular sites. The consultation therefore made recommendations covering both the use and the conservation of forest genetic resources.

The recommendations are of two categories: "general" and "technical." General recommendations call primarily for increasing financial resources and staff and for strengthening the collaboration of governmental, international and research organizations. Technical recommendations are directed to individual researchers.

## General

1. The Consultation *noted* that, in response to a recommendation made at the Second World Consultation, assistance to developing countries in their tree improvement programmes from multilateral and bilateral agencies has increased considerably over the past eight years, but was still less than real needs. In recognition of the importance of such programmes, the Consultation *recommended* that multilateral and bilateral aid agencies should further continue and expand their assistance in this field. In particular, there is still need for more assistance in the form of specialist advice, training courses and fellowships.

2. The Consultation *noted* with satisfaction the increased understanding of the role of forest genetic resources conservation as a dynamic component of forest management and forest utilization. It *recognized* the need for more training in gene resources management and *encouraged* national organizations and bilateral and multilateral aid agencies to give more emphasis to this subject in existing training programmes, and to organize more short-term regional training courses, particularly in tropical countries.

3. The Consultation *warmly welcomed* the new international project on Conservation of Forest Genetic Resources (1108-75-05), which is being financially supported by the United Nations Environment Programme (UNEP) and administered by FAO. It *noted* with approval the action being taken under the project in the establishment of *ex situ* conservation stands of selected provenances of valuable species, in a variety of environments, and the new opportunities these will offer for the expression of existing genetic diversity, and for the development of new gene combinations in harmony with the new environments. It *recommended* that UNEP give high priority to the continuation and expansion of this action.

4. The Consultation *warmly welcomed* the increased activity in the conservation of natural ecosystems throughout the world and *recommended* that close liaison be maintained between FAO and the International Union of Forestry Research Organizations (IUFRO) (Subject Group S2.02). The International Union for the Conservation of Nature and Natural Resources (IUCN) and the United Nations Educational, Scientific and Cultural Organization (Unesco), especially its Man and the Biosphere programme 8, to ensure the provision of professional advice on the selection and management of suitable areas of forest for the conservation and ultimate utilization of their genetic resources.

5. The Consultation *noted* with satisfaction the continued work of the FAO Panel of Experts on Forest Gene Resources, its preparation, initiation and central direction of the Global Programme for Improved Use of Forest Genetic Resources, and its coordination of the international programmes of exploration and seed collection being carried out by research institutes in various parts of the world. It *recommended* the strengthening of the central coordinating role of FAO, to make better use of opportunities for the collection and distribution of information and research material needed for effective exploration, conservation and evaluation of genetic resources.

6. The Consultation *recognized* the great potential value of a coordinated, overall appraisal of internationally replicated provenance trials and that, for this purpose, uniform description of test sites, standardization of traits to be assessed, and uniform methods of measurement are necessary. It *recommended* that international coordinating organizations issue guidelines for the establishment, management

and recording of the trials, and encourage research organizations to work toward achieving such uniformity at least on a regional level. The Consultation also *noted* the value of periodic visits to all trial sites by experienced international, or regional, assessment officers to facilitate overall appraisal and to assist in the local evaluation of individual trials, and *urged* concerned organizations to provide the requisite staff and finance for such assessments.

7. The Consultation further *recognized* that in many countries the planting of trees yields benefits other than wood, for example food and fodder, and environmental and aesthetic benefits in both urban and rural areas. It *recommended* that governments establish and assess species and provenance trials with such other purposes in mind in order to provide material for further genetic improvement.

8. *Noting* that provenance trials established in various tropical and subtropical regions have concentrated on introduced species, particularly on conifers and eucalypts, the Consultation *urged* governments and international organizations to widen the range of species tested to include more studies on the genetic potential of tropical hardwoods and of species for semi-arid regions as identified by the FAO Panel of Experts on Forest Gene Resources. It further *encouraged* research workers and forest managers to make suggestions on additional species to be included in such studies.

9. *Noting* that the IUFRO Congress (XVI) recommended that "increased efforts are required to establish international cooperation in breeding for high yield and disease resistance" the Consultation *recommended* that governmental, regional, international and private organizations intensify their efforts to establish regional and international cooperative breeding programmes for the production of selected or improved seed of individual species of wide importance (e.g., *Pinus caribaea* in the tropics and *Pseudotsuga menziesii* in North America and Europe). Such efforts should provide for research and training of personnel to support breeding programmes and, where appropriate, should include seed orchards producing seed for international use. Recognizing the complexity of cooperative breeding programmes and the need to ensure their continuity, the Consultation further *urged* that they include the provision of full-time managerial staff.

10. The Consultation *recognized* the dynamic nature of breeding and of gene resources management and noted the susceptibility of long-term tree breeding programmes to the destructive effects of reduced financial support. The Consultation therefore *urged* governmental and other organizations to provide continued, consistent financial support.

11. Recognizing that research workers and operational foresters require up-to-date information on international provenance trials and breeding programmes, the Consultation *recommended* that international coordinating organizations refine and adapt computer-based systems for information storage, retrieval and analysis of the requisite data, which would include not only bibliographic material but also original and summary data on trees and sites from individual experiments and projects. The Consultation further *urged* cooperating institutes and organizations to increase the dissemination of such information for the use of individual workers.

12. The Consultation *stressed* that effective programmes well suited to the objectives of sponsoring agencies require the guidance of well-defined goals and comprehensive strategies. It *recommended* that governments and other concerned organizations continually and critically review the goals and breeding strategies of all tree improvement programmes, especially new ones. Increased cooperation between economists and geneticists would aid in such assessments.

13. The Consultation *recognized* the importance of identifying the origin of plant material, of assuring the repeatability of collections and noted that the trade in plant material is increasing. It *recommended* that governments and international organizations intensify their efforts to implement certification schemes to guide this trade.

14. The Consultation *noted* that procedures did not exist for the efficient handling and storage of seed of several economically important forest tree species. Such procedures are required for use in operational forestry, genetic improvement programmes and measures aimed specifically at conservation of gene resources. The problem related to species in most regions of the world but particularly to some important tropical species, which may have a very short period of viability. The Consultation accordingly *recommended* that bilateral and multilateral finance be provided for strong research programmes aimed at developing the required seed handling and storage procedures, especially for tropical species.

15. *Recognizing* the great benefits derived from this and previous consultations, the Consultation *recommended* that a fourth meeting be held within ten years. The time and place should be decided jointly by FAO and IUFRO in the light of any offers to host the meeting which may be received.

**Technical**

1. *Recognizing* the lack of information on a number of species, the Consultation *recommended* that more emphasis be placed on obtaining basic information on the reproductive biology of genetically little known, unimportant species, particularly tropical conifers and hardwoods. Emphasis should be placed on physiological research in relation to the difficulties which occur due to the new environmental conditions of planting.

2. The Consultation *noted* that international provenance trials are commonly assessed for survival, growth and form but *recommended* that these assessments be supported by phenological observations and laboratory studies on physiological, morphological and biochemical traits and wood quality.

3. The Consultation *stressed* the need for a better understanding of the physiological factors involved in genotype environment interaction, par-

ticularly in relation to sites where factors like cold, drought and nutrient deficiencies are limiting, since increasing use will have to be made of such sites in the future.

4. *Recognizing* the need for information on the degree of genetic improvement attained from tree improvement programmes, the Consultation *recommended* that more emphasis be placed on assessing realized gains. This should be done by comparing products of tree improvement programmes with well-defined commercial checks in experiments with replicated plots large enough to eliminate competitive effects. Non-wood benefits, for example erosion control, should not be neglected in assessing gains.

5. More research should be devoted to the methodology of introducing resistance genes into populations already improved for other characters.

6. In view of the potential of vegetative propagation for research, for the mass production of improved genotypes, and as a tool for conserving the genes of trees which are to be removed, research on this subject should be accelerated. Remarkable results have been obtained with the production of cuttings of conifers such as *Picea abies* and *Pinus radiata*, but also of tropical genera such as *Eucalyptus*, *Terminalia* and *Triplochiton*. Better understanding of the effects of juvenility and ageing is an essential prerequisite for further advances in vegetative propagation. The Consultation *welcomed*, therefore, the increasing tempo and promising results of research on tissue and organ culture which were reported.

7. While *noting* that most analyses of tree improvement programmes have shown favourable economic returns, the Consultation *cautioned* that the economics of each breeding programme, especially new ones, should be analysed individually. At a minimum, detailed costs should be recorded for each phase of a programme.

8. The Consultation *stressed* the importance of "widening" economic analysis of tree improvement programmes to include estimates not only of financial but also of net social benefits.

# Progress on general recommendations made by the second World Consultation on Forest Tree Breeding, Washington, 1969

The second World Consultation on Forest Tree Breeding made a number of general and technical recommendations. This paper reports on progress made on each of the general recommendations, as of October 1976. As information was lacking in some areas, participants are invited to inform the Secretariat of any significant progress which is not adequately covered by this report.

1. RECOMMENDATION: Tree improvement has an essential part to play in countries where afforestation is becoming increasingly important. In the tropics and subtropics, where growth rates are frequently high, gains from tree improvement may be rapid and substantial. The Consultation noted with satisfaction the development of forest genetics and tree improvement programmes in tropical countries since the first World Consultation on Forest Genetics at Stockholm in 1963. The value of such planned programmes to the economies of tropical countries was reiterated and their continuation and expansion recommended.

PROGRESS: Progress has continued, and at least 20 tropical countries now have tree improvement programmes. Early efforts were largely devoted to the identification of plus trees and the establishment of seed production areas, but emphasis is now shifting to the establishment of seed orchards. Provenance research is being conducted on a much greater scale.

2. RECOMMENDATION: In recognition of the importance of tree improvement programmes in developing countries, multilateral and bilateral aid agencies should continue and expand their assistance in this field. In particular, there is need for more assistance in the form of specialist advice, training centres and fellowships.

PROGRESS: Since 1969, FAO has provided tree breeders to work on FAO/UNDP projects in Bangladesh, Brazil, Colombia, Cuba, Indonesia, Iraq, Madagascar, Malaysia, Nigeria, and Turkey, while a much larger number of countries have received assistance in species and provenance trials, and seed procurement. Some of these projects provided fellowships for training in tree improvement and species research.

A number of countries have benefited from bilateral arrangements for assistance in tree improvement, for example, India and Thailand (Danish aid), Nigeria (United Kingdom), and Congo (France).

Successful training courses on forest tree improvement were held in Hungary (1971), Kenya (1973), and Australia (1977), and one on forest seed collection and handling in Thailand (1975).

3. RECOMMENDATION: The Consultation considered that there was now sufficient evidence to justify the wide application of the results of genetics research to forestry practices. Government services were, therefore, urged to sustain or enlarge programmes for the mass production of genetically superior trees revealed as suited for use in forest and urban environments.

PROGRESS: Although a number of governments have expanded programmes for mass producing superior trees and others have initiated new programmes, the pace of reforestation, particularly in developing countries, still far exceeds the supply of improved seed.

4. RECOMMENDATION: More attention should be paid to breeding forest trees for products other than wood (e.g., tannin, seeds and fruits, honey and beeswax) and for environ-

mental benefits such as soil stabilization, shelterbelts and aesthetic values. Particular attention should be given to trees to be grown to provide social benefits and amenity values in urban areas.

PROGRESS: Little progress has been made in breeding better trees for soil stabilization, shelterbelts and most other non-wood products, although a few developed countries have made some improvement in trees for urban areas, resin and tannin. Greater attention in urban tree breeding is now being given to improving resistance to diseases and tolerance to abiotic stresses.

5. RECOMMENDATION: The Consultation recommended to the Food and Agriculture Organization of the United Nations (FAO), the International Union of Forestry Research Organizations (IUFRO), the International Union for the Conservation of Nature and Natural Resources (IUCN), and the International Biological Programme (IBP) that they: (*a*) urge governments and institutions to take action forthwith to protect and conserve the germ plasm of forest tree species and provenances that are in danger of extinction; and (*b*) collaborate in compiling directories of forest tree species and provenances in danger of extinction, and of nature reserves, parks, etc., where native forest trees are being conserved.

PROGRESS (*a*): The UN Conference on the Human Environment held in Stockholm in 1972 stressed the need for governments to take effective action to preserve the world's genetic resources, and made specific reference to forestry species. One of the results of the meeting was the formation of the United Nations Environment Programme (UNEP); genetic conservation is one of its primary concerns.

Specific proposals for a global programme for improved use of forest genetic resources, including conservation, were drawn up in 1974 by the FAO Panel on Forest Gene Resources. More detailed guidelines on *in situ* and *ex situ* conservation were contained in the 1975 FAO/UNEP pilot study entitled, "The Methodology of Conservation of Forest Genetic Resources". A start at implementing the global programme has been made through the current UNEP-financed project on "Conservation of Forest Genetic Resources". Some seed and funds have already been distributed for the establishment of provenance conservation stands of tropical pines and eucalypts in developing countries in the tropics, and for the collection of substantial quantities of seed of additional species and provenances for conservation.

Unesco also has been very active in encouraging germ-plasm conservation, including forest tree species. Following on the work of the IBP (which was terminated in 1974), the Unesco programme for Man and the Biosphere (MAB) project 8 published in 1974 "Criteria and Guidelines for the Choice and Establishment of Biosphere Reserves", and as of September 1976 more than 40 countries had proposed over 200 areas as part of the international network of "biosphere reserves". This network is intended to 1) combine the ecological preservation of representative ecosystems with research into their functioning, 2) investigate man's impact on natural systems, and 3) develop the means to monitor this impact.

PROGRESS (*b*): With regard to directories of forest tree species and provenances in danger of extinction, in 1970 and 1971 IUCN issued data sheets on endangered and rare species for inclusion in its "Red Data Book," Volume 5, on Angiospermae. Volume 5 of the "Red Data Book" is now under revision and is to be issued under the new title, "Plants."

In addition, IUFRO working party, S2.02-02, on gene resource conservation, has begun to prepare data sheets on tree species undergoing genetic impoverishment, but not sufficiently endangered to warrant inclusion in the "Red Data Book." All tree species are to be considered, but particularly those of economic importance as sources of wood, food or fodder. Seventeen species have been covered to date.

Also, among the tree species listed by the FAO Panel on Forest Gene Resources for priority action in the global programme, are 25 which were identified as being endangered with extinction or severe depletion of the gene pool.

Regarding nature reserves and parks where native forest trees are being conserved, IUCN published in 1971 the second edition of its "United Nations List of National Parks and Equivalent Reserves," and up-dated it through 1975. This provided the basis for an expanded version under the title, "World Directory of National Parks and other Protected Areas," consisting of data sheets on the areas' conservation status, which have been published in instalments since 1975. Under the auspices of IUCN, two studies comparing *in situ* conservation needs to achievements were also prepared: "The Distribution of Protected Areas in relation to the Needs of Biotic Community Conservation in Eastern Africa," and, "Conservation Review of Tropical Rain Forests: General Considerations and Asia."

A Unesco directory of biosphere reserves is also planned.

6. RECOMMENDATION: The working groups of IUFRO provide a valuable means of promoting international cooperation, but the Consultation felt that certain needs were not being met by the working groups presently existing. IUFRO was requested to establish additional working groups dealing with tropical pines and hardwoods; hybridization among species and provenances; and damage to trees by cold, drought and other environmental extremes.

PROGRESS: In 1971, a reorganization of the research units of IUFRO was undertaken. There are six divisions. Division 2 deals with forest plants and forest protection, and contains eleven subject groups and three project groups, including: physiology (S2.01); species, provenances and gene resources (S2.02); breeding (S2.03); genetics (S2.04); genetic resistance to insects and disease (S2.05); and air pollution (S2.09). Among the many working parties are those on tropical species provenances (S2.02-08); eucalypt provenances (S2.02-09) and breeding tropical species (S2.03-01). Also, under the two tropical working parties, *ad hoc* action groups have

been set up on *Gmelina arborea*, *Tectona grandis*, tropical hardwoods genetics, tropical eucalypts, Araucarias, selection and breeding populations, provenance trials, international provenance trials economics, distribution maps, seed data, and *Triplochiton scleroxylon*.

7. RECOMMENDATION: The establishment of several regional centres for seed collection and distribution, such as those operating at Canberra, Oxford (England) and Humleback, or proposed for Macon (U.S.A.) and Mexico, was greatly welcomed. Such regional centres were necessary for the introduction of new variations, for study of inherited variation, and for conservation of gene resources. Early attention should be given to the possibilities of setting up additional regional seed centres, especially in western Africa and South America.

PROGRESS: Considerable progress has been made at the national rather than the regional level; most countries have set up national seed co-ordinating centres to which requests for seed can be directed. The seed centres in Macon (U.S.A.) and Mexico have become operational and both have been instrumental in collecting and distributing research quantities of source-identified seed.

8. RECOMMENDATION: The Consultation endorsed FAO's efforts to coordinate and support regional programmes for seed collection, involving also the establishment of an Advisory Panel of Experts on Forest Gene Resources. A wider geographical representation ought to be provided by including on the panel specialists from Asia, West Africa, South America and eastern Europe. The Consultation also endorsed the action programme proposed by the panel but stressed that increased financial support would be needed, both from national and international sources, to implement such a programme. It would be useful for FAO to publish periodically in UNASYLVA the latest information on availability of provenance seed collections and on proposed seed collection expeditions.

PROGRESS: Membership in the FAO Panel on Forest Gene Resources has been expanded to include representatives from Asia, South America and West Africa, but does not yet include a member from eastern Europe. The Panel has met three times since the last Consultation (in 1971, 1974 and 1977). The original action programme drawn up by the Panel has now been incorporated into the more ambitious "Proposals for a Global Programme for Improved Use of Forest Genetic Resources," and some additional funds have been obtained.

News of provenance seed collections is reported in a new FAO publication started in 1973 called, "Forest Genetic Resources Information," which is issued about twice annually in English, French and Spanish.

9. RECOMMENDATION: IUFRO, in collaboration with FAO, was requested to publish a paper on the practical, administrative and costing aspects of seed-collecting expeditions.

PROGRESS: The following papers, with emphasis on the practical aspects of seed collecting, can be mentioned:

— Barner, H., "Procurement of Douglas Fir Seed for Provenance Research," 15th IUFRO Congress, 1971.

— "Report on the FAO/DANIDA Training Course on Forest Seed Collection and Handling," FAO, 1975.

— Dobbs, R.C. *et al.*, "Guidelines to Collecting Cones of B.C. Conifers," British Columbia Forest Service/ Canadian Forestry Service, Joint Report No. 3, 1976.

Forest Genetic Resources Information also reports on seed-collecting expeditions.

10. RECOMMENDATION: Professional forestry societies were asked to incorporate into their codes of ethics provisions which emphasized the personal responsibility of foresters engaged in planting or seeding: (*a*) to obtain and record exact information on the provenance, primary or secondary, of the planting stocks or seeds used; and (*b*) to do their utmost to provide and use only seed or plants of provenances best suited to the local environment. All practising foresters should regard meeting these responsibilities as a moral obligation.

PROGRESS: The spirit of this recommendation merits reiteration, but it is not known to what extent implementation has been pursued.

11. RECOMMENDATION: The Consultation recommended that the seed certification scheme of the Organisation for Economic Co-operation and Development (OECD) be extended to all countries as a means of providing a uniform system for the identification and control of genetic identity of all forest reproductive material.

PROGRESS: The latest version of the "OECD Scheme for the Control of Forest Reproductive Material Moving in International Trade" was issued in 1974. It provides a useful set of guidelines on seed certification and related matters but, so far, implementation has been disappointing. It is now likely, however, that the scheme will be accepted by the EEC (European Economic Community) and implementation in all EEC countries may be expected by the end of 1977. Participation of other countries in the scheme is voluntary.

12. RECOMMENDATION: IUFRO was requested to investigate the possibilities of developing and using an international system for rapid retrieval of information from tree breeding literature and experiments, and for standardizing, integrating and mechanizing character evaluation for tree breeding research, as is being done for crops research.

PROGRESS: The computerized information storage and retrieval system for international tropical provenance experiments (INTFORPROV) developed by CFI, Oxford, is a major advance in this field, but there is still need for a similar, more comprehensive system for forest genetic resource conservation. With financial contributions from the Consultative Group for International Agricultural Research (CGIAR), and guidance from the International Board for Plant Genetic Resources (IBPGR), FAO has begun developing an international genetic resources communication, information and documentation system (GR/CIDS) for agricultural crops. The IBPGR has indicated that it supports extension of GR/CIDS to forestry, but detailed

study of the desirability and feasibility of this has not yet been possible.

13. RECOMMENDATION: Administrators of forestry research agencies and of tree breeding programmes were urged to review the working relationships between geneticists and scientists in other disciplines, in order to provide opportunities for that meaningful multidisciplinary cooperation required to attain the goals of breeding for resistance to pests and environmental extremes, for wood quality and for other traits. Furthermore, broad systems analysis should be applied to breeding programmes to define criteria, values and operating systems.

PROGRESS: No report.

14. RECOMMENDATION: International organizations such as FAO, IUFRO and the European Economic Community (EEC) were asked to lend increased effort to coordinating the work of tree breeders on the regional plane, especially in respect to common species.

PROGRESS: Regional coordination of tree improvement programmes in North America is effected through the FAO North American Forestry Commission, but no similar arrangements exist for other forestry commissions.

15. RECOMMENDATION: In order to assure the most efficient use of the limited scientific and professional persons experienced in tree breeding, governments and organizations were urged to provide support by taking into employment technicians who could undertake much of the routine burden of tree breeding programmes.

PROGRESS: No report.

16. RECOMMENDATION: Important research results should be published in periodicals of wide circulation. Papers which have only local distribution should be sent to the Commonwealth Forestry Bureau for notice in *Forestry Abstracts*. Authors and editors of professional magazines were urged to include in published results such vital data as genetic variances, selection intensity, genotypic and phenotypic correlations between traits, experimental design and the error of the estimates, which have in the past frequently been omitted.

PROGRESS: No report.

17. RECOMMENDATION: The Consultation requested IUFRO to stimulate and hasten the publication of monographs on the genetic characteristics of important forest tree species, on the lines of those published by the Society of American Foresters and by the Commonwealth Forestry Institute, Oxford, England.

PROGRESS: The publication programmes of both the SAF and CFI have remained active. The genetics of many of the most important North American forest species have now been covered in the monograph series, while the CFI has issued three additional monographs in their Tropical Forestry Papers series.

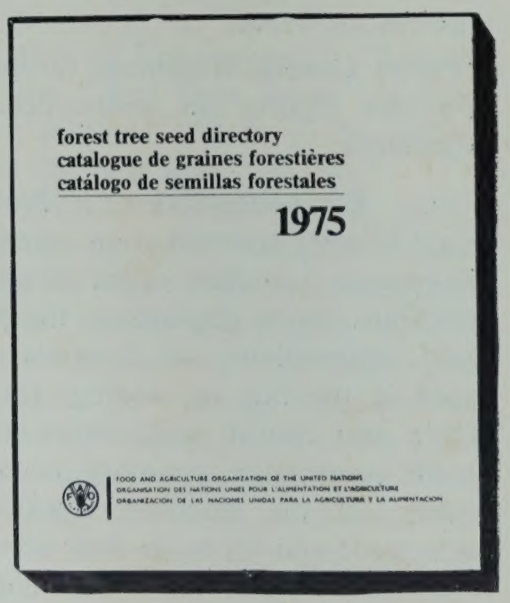
18. RECOMMENDATION: The Consultation noted the inclusion in the FAO Programme of Work and Budget for 1970-71 of revised editions of the FAO *Forest Tree Seed Directory* and of the *World Directory of Forestry Research Institutes*. It recommended that these revisions be quickly completed. The new *Forest Tree Seed Directory* should include information on seed certification schemes in operation and on the seed suppliers in each country who complied with these schemes.

PROGRESS: A trilingual (English, French and Spanish) revised edition of FAO's *Forest Tree Seed Directory* was issued in 1975. As the result of a recommendation by FAO's Committee on Forestry, the Directory was simplified to provide information only on the availability of species, and varieties when known, by countries and the address of one national seed coordinating centre in each country to which inquiries can be addressed. The Directory does not list seed provenances, particular certification schemes or private suppliers.

Revision of the *World Directory of Forest Research Institutes* was eventually not approved by FAO's governing bodies, and was deleted from the Programme of Work and Budget on the grounds that the information quickly becomes outdated.

19. RECOMMENDATION: Recognizing the great benefits derived from this and the preceding consultation, the Consultation recommended that a third meeting be held about 1975. Appreciation was expressed for the unofficial invitation to hold the next gathering in Australia, but at the same time strong support was given to the idea of having the meeting in a developing region having a tree breeding programme in the tropics or subtropics. The agenda should be restricted to a limited number of topics that could be explored in depth.

PROGRESS: Meeting held March 1977.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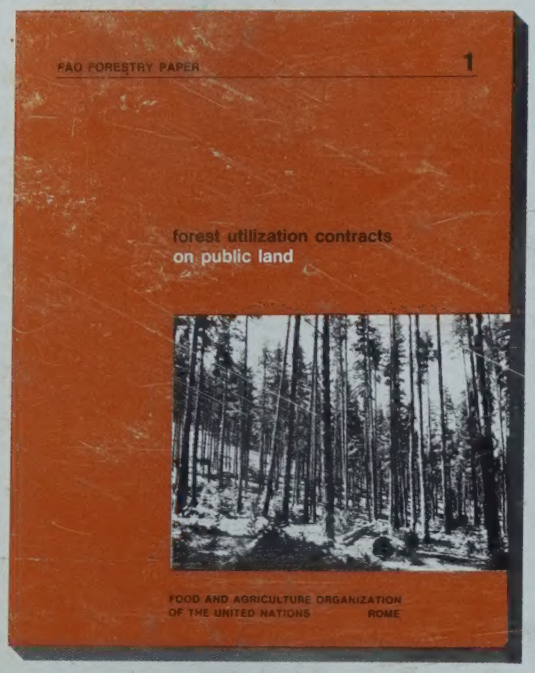


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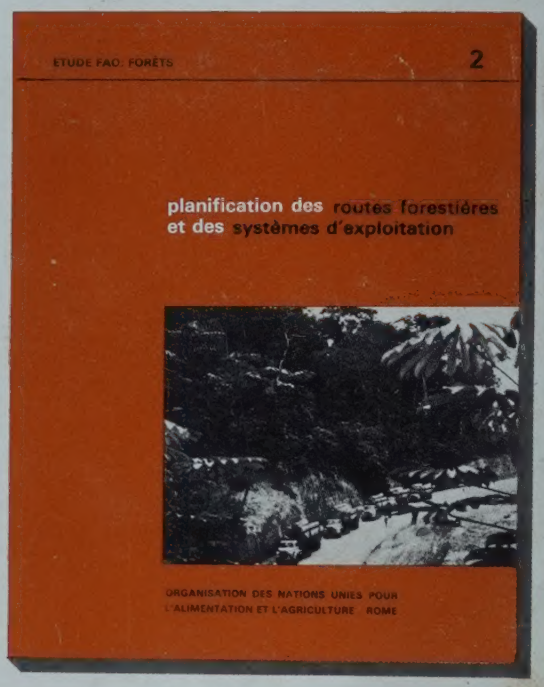


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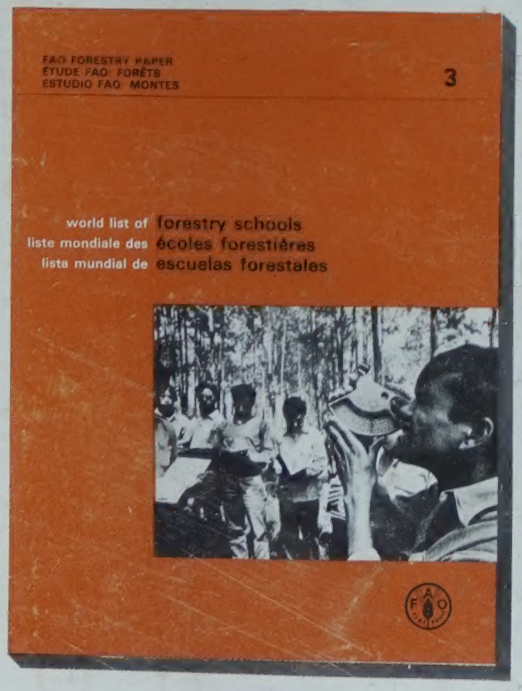


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